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Apparent Abundance, Distribution, and Migrations of Albacore, Thunnus alalunga, on the North Pacific Longline Grounds

By

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ABSTRACT

This paper considers the dynamics of albacore, Thunnus alalunga, on the Japanese North Pacific longline grounds. In addition to changes in apparent abundance and distribution, the modes of immigration and emigration from the longline grounds are considered in terms of the migratory route of the albacore in the North Pacific Ocean. The data show a clear decline in apparent abundance on the longline grounds during the 1949-61 study period. This decline could not be related to changes in the average size of the fish or fishing effort. Spatial statistics were computed to describe the distribution of the albacore on the longline grounds. These show very clear cyclical changes each year. These changes reflect a net southwest movement of the two-dimensional first-moment at a velocity of about 6.5 miles (12 km.) day^{-1}. The second order spatial statistics showed a maximum longitudinal expansion and latitudinal contraction during the peak of the fishing season. The time-space coordinates of the two-dimensional first-moment of the albacore distribution appear to be highly predictable. The migration route of the albacore among North American, pole-and-line, and longline fisheries is considered. It appears that the dynamically most significant movement of albacore is from the North American fishery, to the pole-and-line fishery, to the longline fishery.

INTRODUCTION

The albacore, Thunnus alalunga, of the Pacific Ocean apparently comprise two populations. One of these populations lives south of the Equator and has been fished by the Japanese longline fishery at a relatively low intensity from the early 1950's until 1956. After 1956 the intensity of longline fishing for albacore in the South Pacific Ocean increased substantially; this increase has been documented by Otsu and Sumida (1968). The other population--the subject of the present paper--lives in the North Pacific Ocean. It has been exploited by Japanese since the inception of the Shōwa Era in 1926 (Nakamura, 1951: p. 14 in English translation).

In the 1950's, there were essentially three fisheries for albacore in the North Pacific Ocean: (1) the summer troll and pole-and-line fisheries by United States and Canadian fisher-

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men off the coast of North America, (2) the winter longline fishery by Japanese in the western North Pacific Ocean, and (3) the spring pole-and-line fishery by Japanese in the western North Pacific Ocean. We shall call these the North American, the longline, and the pole-and-line fisheries, respectively. Figure 1 shows the location of each of these fisheries, and figure 2 shows the relative importance of each in terms of landings. Much of the literature in English can be found in the description of the North American fishery in Clemens and Craig (1965), of the longline fishery in Suda (1963b), and of the pole-and-line fishery in Suda (1963b) and in Van Campen (1960). The migrations of the albacore among these fisheries have been described, only recently, by Clemens (1961), Otsu and Uchida (1963), and Yoshida and Otsu (1963).

The importance of the albacore to both Japanese and American fishing interests suggested the institution of a cooperative program between Japanese and United States researchers to study this fish in the Pacific Ocean. An exchange of data on the longline fishery for albacore between the Nankai Regional Fisheries Research Laboratory (now a part of the Far Seas Fisheries Research Laboratory at Shimizu) and the Bureau of Commercial Fisheries was one of the first steps in this cooperative program. The data that we obtained consisted primarily of nominal longline effort (in number of hooks fished) and catch in numbers of albacore. These data were arranged by month and 1° quadrangles of ocean for the years 1949-61. There were albacore catch-and-effort statistics for about 50,000 one-degree squares and months. Unfortunately, the catch statistics for species other than the albacore were not included in the data that were made available to us.

After completing this study we compared our results on CPUE (catch-per-unit-of-effort) with unpublished Japanese data provided to us by Akira Suda and found some disagreement owing to Suda's using a slightly different data set. The differences, however, do not appear to affect materially any of our interpretations or conclusions.

The present paper, then, provides a summary and discussion of these data as they relate to the dynamics of the albacore in the North Pacific Ocean. The paper is divided into three sections. In the first, we describe the decline in apparent abundance of the albacore in the 1950's; in the second, we provide spatial statistics for the distribution of albacore in the longline fishery; and in the third, we provide evidence that indicates that the predominant migratory route of the albacore is from the North American to the pole-and-line to the longline fishery.

APPARENT ABUNDANCE

Apparent abundance will be considered from two points of view. First, the long-term trends in CPUE will be considered. Second, the deviations from these trends will be considered.

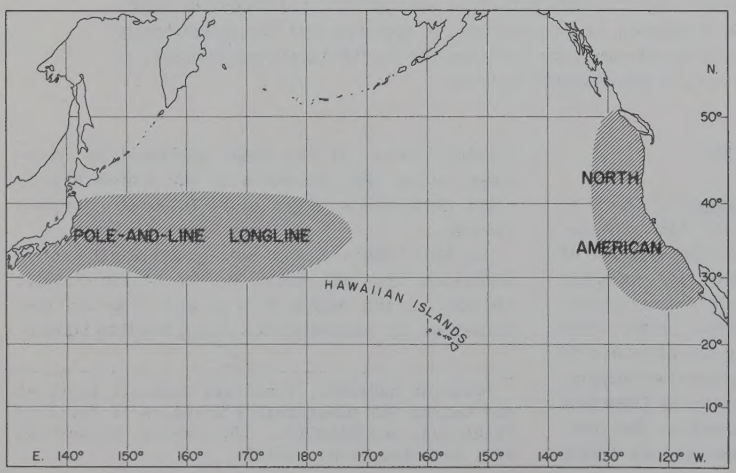

Figure 1.--Approximate location of the North American, longline, and pole-and-line albacore fisheries.

Long-term Trends in Catch-per-unit-of-effort

The catch-per-hundred-hooks is CPUE and an index of apparent abundance for the albacore on the North Pacific longline grounds. This section provides indices that are used to estimate trends in apparent abundance for the longline fishery.

In developing the indices we first considered the use of the ratio of averages CPUE statistic versus the average of ratios CPUE statistic. (The ratio of averages CPUE statistic is computed by dividing the total catch by the total effort, whereas, the average of ratios CPUE statistic is computed by averaging individual CPUE ratios.) These two statistics are plotted for a typical Marsden square in the longline albacore region as a time series (fig. 3). Figure 3 shows that the ratio-of-averages statistic approximates the average-of-ratios statistic during the nonpeak fishing months, but during the peak fishing months the ratio-of-averages statistic generally exceeds the average-of-ratios statistic. The latter situation (see Gulland, 1955) indicates that the fishermen are concentrating their effort upon the fish (or the fish are becoming more vulnerable in the most heavily fished areas). We note, however, a tendency for the average of ratios to exceed the ratio of averages in months of relatively high apparent abundance in some of the terminal years of the time series. We do not know whether this reversal in the relation between the average-of-ratios statistic and the ratio-of-averages statistic reflects a shift in fishing emphasis from albacore to another species such as bluefin tuna or to a response to a general decrease in the apparent abundance of albacore. We decided to use the average-of-ratios statistic in our analyses since (1) it shows roughly the same declining trend as the ratio-of-averages statistic, (2) it is unweighted by the distribution of effort, and (3) by virtue of the central limit theorem it is more amenable to the normality assumptions of regression analysis (which will be used subsequently).

The variability of the CPUE index and also the effects of the varying relation between the two ratio statistics were reduced by taking advantage of the rather well-defined (especially when contrasted with trends in apparent abundance of tunas in the low latitudes) seasonal periodicity of albacore CPUE. This well-defined seasonal periodicity reflects a fairly consistent correlation among the monthly CPUE's for any year. For example, the CPUE in January is always relatively high whereas the CPUE in July is always relatively low. This consistent ranking suggests that the variability in a composite annual CPUE index can be considerably reduced by not averaging the monthly CPUE's for each year, but rather by studying the trends among Januaries, among Februaries, and the rest of the months. We assume from examining our data that the errors induced by any lack of synchrony (see fig. 3 for typical example) among the annual CPUE cycles are relatively small. We also assume that most of the information pertinent to long-term changes in apparent abundance is contained in the data for the midwinter months at the peak of the fishery.

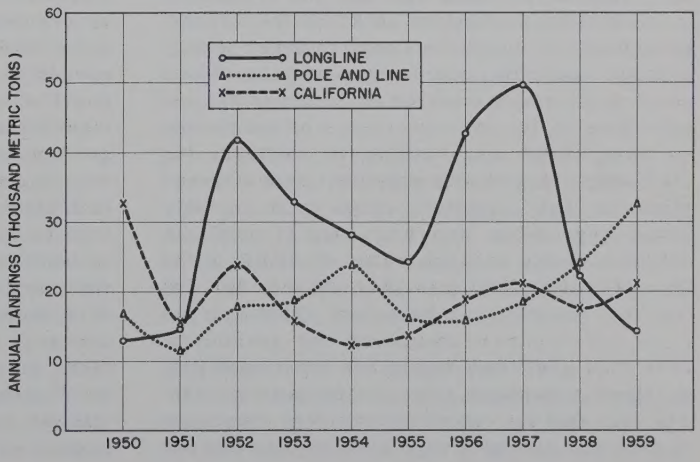

Figure 2.--Albacore landings taken by various fisheries in the Pacific Ocean, 1950-59 (from Yoshida and Otsu, 1963: p. 317).

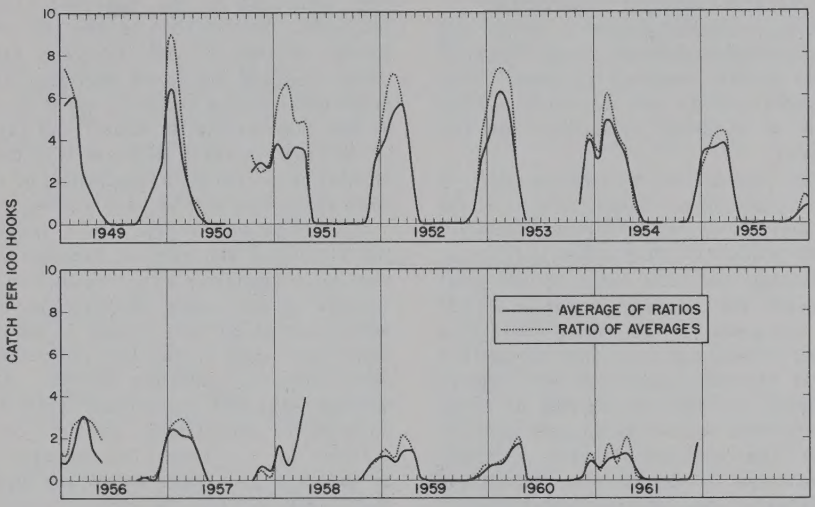

Figure 3.--Catch-per-hundred-hooks (in number of fish) computed as an average-of-ratios statistic and a ratio-of-averages statistic for each month in Marsden square 130 (lat. 30°-40° N., long. 140°-150° E.), 1949-61.

Thus we examined the trend in CPUE over the years for each January, each February, etc. Examination of this trend was accomplished by computing for each month linear and quadratic regression of average CPUE on year for each Marsden square that had observations on a sufficient series of years to warrant study. The Marsden squares that contained a sufficient series of data define the albacore grounds and are bounded by lat. 20° to 40° N. and long. 130° E. to 170° W. The quadratic regressions exhibited significant reduction (at the 5-percent level) in sum of squares in 23 of the 112 regressions. Owing to the small number of significant quadratic regressions and the closeness of the average values of the quadratic regressions to the average values of the corresponding linear regressions we decided, for simplicity, to consider only the linear regressions in our analyses. Thus each month's linear regression line was used to obtain an estimate of the average value of CPUE at the time of initial fishing in 1949 and for 1961, the last year for which we have data. This average value for apparent abundance was greater in 1949 than 1961 with only a few exceptions (fig. 4); these exceptions were for nonpeak months. The fact that the estimated apparent abundance in 1949 was almost always greater than that for 1961 indicates that except for the few noted exceptions all of the slopes were negative and that, on the average, apparent abundance declined throughout the study period.

We also considered the problem of evaluating the variability associated with each regression relative to the magnitude of the slope for each regression. We realized a priori that in instances many of the regression slopes would not be significantly different from zero owing to the small sample sizes (a maximum of 14 data points for each regression). Significant differences from the hypothesis of zero slope were determined by the usual t-test at the 5-percent level. We note--with respect to the usual assumptions involved in these tests of significance--that each datum is based on an average so the probability distribution of the data must tend toward a normal distribution; that since the sample sizes within each month tend to be approximately equal, the assumption of homogeneity of variance appears to be fairly well approximated; and that consideration of each month separately tends to favor independence of errors among the data. We conclude from the consistently negative slopes and the small sample sizes that the percentage of significant slopes (29 percent) would increase if sample sizes could have been larger, suggest-

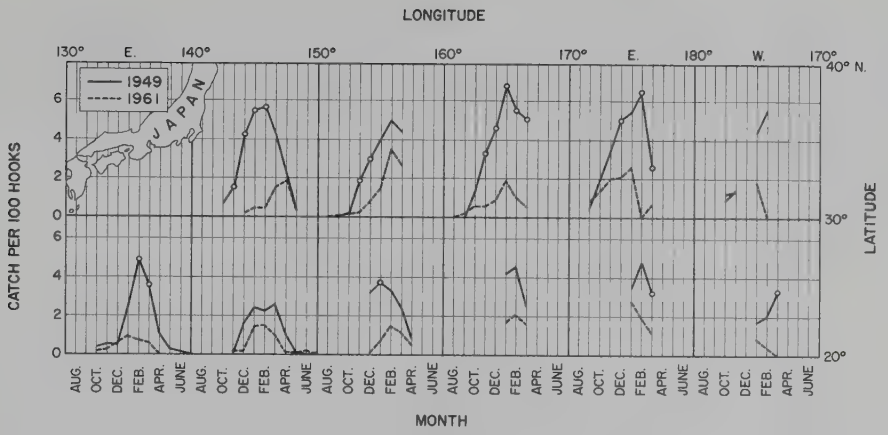

Figure 4.--Estimated average apparent abundance of albacore (in numbers of fish caught per hundred hooks) in 1949 and in 1961 for Marsden squares 90-95 and 126-130. Circles denote slopes that were significant at the 5-percent level.

ing that there was a real reduction in CPUE over the study period.

In order to express the decline in abundance for the entire longline fishery we averaged the slopes and intercepts over the fishing area shown in figure 4 for those months (January, February, and March) for which the data were most abundant. Averaging was accomplished by weighting each slope and intercept by the inverse of its variance. The weighted averages along with the statistics used to compute them are set forth in table 1. We note that the weighted average intercept is at its peak in February, having an average value of 4.13 albacore per hundred hooks. The weighted average slopes are remarkably similar, especially considering the many possible sources of variation. There is an average loss of about 0.2 fish per hundred hooks per year. Thus the February CPUE of 4.13 albacore per hundred hooks would be reduced, after 13 years, to a value of 1.53 fish per hundred hooks, indicating a nearly 60-percent reduction in apparent abundance and implying a corresponding decrease in actual abundance. If we treat the February CPUE as a simple index and assume that the trends in apparent abundance actually reflect trends in actual abundance, then a reduction of 0.2 fish per hundred hooks per year in apparent abundance would provide us with a crude estimate of the increase in the per-head rate of death of 0.1 per year. This increase places the total instantaneous mortality coefficient of the albacore in the longline fishery at a minimum value of 1.3 at the end of the 13-year study period. If we apply this mortality coefficient to the yield isopleths computed by Suda (Kamimura, 1966: p. 765) and if our assumptions are reasonable, either a reduction in fishing intensity or an increase in recruitment size would probably produce an increased yield per recruit on the longline fishing grounds.

If total mortality did, in fact, increase on the albacore longline grounds, during the study period, then, all other things being equal, we should expect a decrease in the average age and consequently in the average size of albacore taken on the longline ground. Such a reduction in average age was indicated by Suda (1959) and can also be seen qualitatively in another paper by Suda (1963b: p. 1250). On the other hand, we have computed the average lengths of the albacore for the North American (the California fishery), the longline, and the pole-and-line fisheries from data given by Clemens and Craig (1965) and Suda (1963a). We have plotted these data in figure 5 and note that a decline in average length for these fisheries is not apparent. We cannot, at present, reconcile the decline in one set of the Japanese data and the lack of a decline in the other.

Deviations from the Long-term Trend

In this section we consider the deviations from the regressions of average CPUE on year for the Marsden squares in the albacore area.

Table 1.--Intercepts (at 1949), slopes, intercept weights (1/variance of intercept), and slope weight (1/variance of slope) used to derive the weighted average intercept and the weighted average slope. These statistics are based on the intercept and slope of linear regressions of average CPUE on year computed for peak fishing months and Marsden squares within the Japanese North Pacific albacore longline ground

Month	Marsden square	Years	Intercept	Slope ($x10^{-2}$)	Weight intercept	Weight slope
		Number				
January	90	10	0.0169	-0.0779	0.1010	-0.1104
	91	12	0.0332	-0.0434	0.0747	-0.0565
	92	11	0.0414	-0.2107	0.0680	-0.0476
	93	13	0.0373	-0.2577	0.1060	-0.1122
	94	13	0.0244	-0.0814	0.0794	-0.0626
	95	14	0.0247	-0.1203	0.1513	-0.2243
	126	10	0.0434	-0.2185	0.0588	-0.0374
	127	13	0.0548	-0.2372	0.0722	-0.0515
	128	13	0.0671	-0.4017	0.0668	-0.0483
	129	13	0.0404	-0.2061	0.0819	-0.0662
	130	14	0.0549	-0.3856	0.1369	-0.1830
			Weighted average intercept 0.0384			
			Weighted average slope $-0.2061x10^{-2}$			
February	90	11	0.0199	-0.1318	0.1436	-0.2102
	91	12	0.0484	-0.2447	0.0663	-0.0432
	92	12	0.0452	-0.1928	0.0676	-0.0449
	93	13	0.0328	-0.1435	0.1363	-0.1814
	94	14	0.0224	-0.0526	0.1350	-0.1713
	95	14	0.0487	-0.3199	0.0888	-0.0734
	126	10	0.0561	-0.5665	0.0446	-0.0161
	127	13	0.0651	-0.5665	0.0583	-0.0326
	128	12	0.0554	-0.3801	0.0659	-0.0428
	129	13	0.0499	-0.1189	0.0835	-0.0670
	130	13	0.0567	-0.4301	0.1100	-0.1171
			Weighted average intercept 0.0413			
			Weighted average slope $-0.2076x10^{-2}$			
March	90	10	0.0327	-0.3460	0.1031	-0.1056
	91	12	0.0311	-0.1614	0.1267	-0.1522
	92	12	0.0244	-0.0725	0.1125	-0.1212
	93	13	0.0246	-0.1084	0.1032	-0.0992
	94	14	0.0261	-0.1209	0.0885	-0.0704
	95	14	0.0367	-0.2320	0.0864	-0.0668
	126	-	No data	-	-	-
	127	10	0.0256	-0.1589	0.1494	-0.2111
	128	11	0.0500	-0.3712	0.0881	-0.0761
	129	13	0.0439	-0.1491	0.0576	-0.0307
	130	13	0.0422	-0.2159	0.0846	-0.0668
			Weighted average intercept 0.0324			
			Weighted average slope $-0.1854x10^{-2}$			

Table 2.--Indices of magnitude of deviations from long-term trend obtained by approximate integration of the deviations shown in figure 6 for December, January, February, and March of each year, 1948-61

1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961
5.5	-7.1	-32.4	-7.5	55.5	38.0	6.5	-24.5	-30.2	-8.5	11.6	-4.5	-6.0	10.5

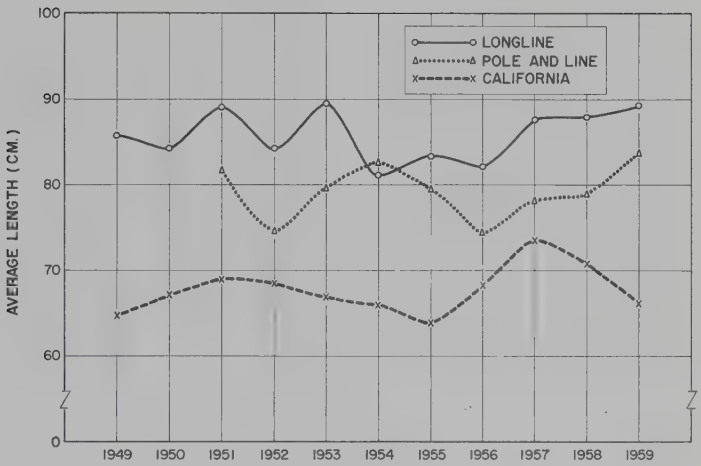

Figure 5.--Average length of albacore taken in various North Pacific albacore fisheries. Data on the longline and pole-and-line fisheries were compiled from Clemens and Craig (1965) and Suda (1963a).

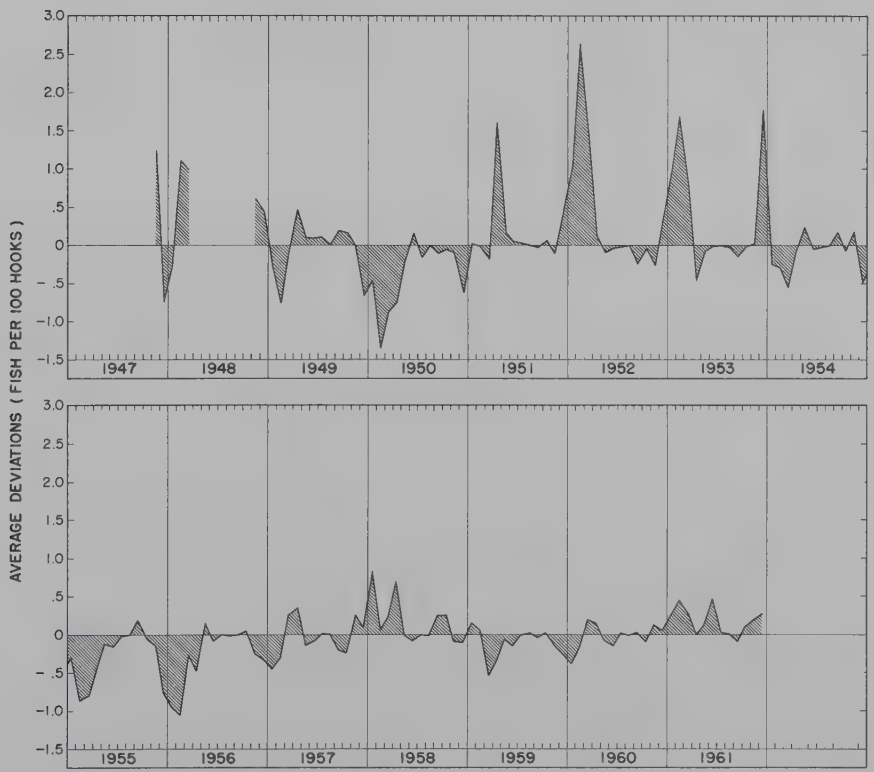

Figure 6.--Average deviations of CPUE for albacore from the regression of CPUE on year for each month from November 1947 to December 1961.

To further condense these data, we averaged for each month the deviations from the linear regressions for the Marsden squares in the albacore area. These deviations are plotted in figure 6. We note from figure 6 that there are, as one would expect, both positive and negative deviations and that these deviations tend to be inversely proportional to time (on a per-annum scale). An index of the magnitude of each year's deviations for the peak fishing period was formed by "integrating" each year's December, January, February, and March deviations. The integration was accomplished by triangular approximation. The indices for each year are given in table 2. We note from table 2 that the greatest negative deviation was obtained in 1950 and the greatest positive deviation in 1952. Furthermore, positive deviations do not appear to be distributed randomly among the negative deviations: In this respect, there are two runs of three negative deviations, one run of three positive deviations, and one run of two negative deviations. These groupings indicate that above-average and below-average years do not occur at random. This phenomenon is most easily explained by strong year classes appearing for more than 1 year in the fishery. It is interesting to observe, however, that the initial year of a run of positive deviations does not correspond with decreased average size of the fish in the longline fishery (fig. 5).

SPATIAL STATISTICS

The spatial distribution of fish in the ocean is customarily studied with the aid of cartographic plots of apparent abundance (see, for example, Nankai Regional Fisheries Research Laboratory, 1959). In some instances, patterns of movement from cartographic plots may be difficult to discern. We have tried to avoid this difficulty in our study of the albacore by examining statistics related to the spatial moments of effort, albacore catch, and albacore CPUE. Thus, we have computed for effort, catch, and CPUE for each month statistics derived from, or equivalent to, the spatial moments--the longitudinal mean, the latitudinal mean, the longitudinal standard deviation, latitudinal standard deviation, and the correlation coefficient between latitudinal and longitudinal positions; these five statistics are called, for convenience, spatial statistics.

The method of computing spatial statistics (i.e., moments or statistics derived from moments) is given in any text on mathematical statistics (e.g., Parzen, 1960: pp. 199-210) and need not be considered in detail here. We simply outline a typical calculation: the latitudinal mean for catch was computed by

$$\sum_{j=1}^{z} j \frac{C_j}{T}$$

where $j = 1, 2, \ldots, z$ degrees of north latitude (z is an arbitrary number greater than the maximum latitude at which albacore are caught); C_j is the total catch (in numbers) of albacore taken in the j-th latitudinal strip; and T is the total number of albacore taken in all of the latitudinal strips. The latitudinal variance of catch is computed simply by squaring j in the above formula and subtracting from this result the square of the first latitudinal moment of catch. The standard deviation is, of course, the square root of the variance, etc.

We now consider several aspects of the North Pacific longline fishery for albacore based on the spatial statistics. These aspects include interpretation of the spatial statistics, periodicities and trends in the spatial statistics, the average location of the spatial statistics, and apparent movement. But first we note that although the spatial statistics were computed for effort, albacore catch, and albacore CPUE, it became apparent that the spatial statistics for catch and CPUE were quite similar and therefore did not, for the North Pacific longline fishery for albacore, in most cases, warrant separate detailed study. It also became apparent that some of the effort included in our data was not, by nature of its spatial location, directly intended to catch albacore. Therefore, because of the similarity between catch and CPUE spatial statistics and the nature of the reported effort, emphasis--in our discussion--is placed on the spatial statistics for CPUE while those for effort are reported mostly to indicate the spatial-temporal nature of the effort distribution included in our data.

Interpretation

A degree of caution must be maintained in the interpretation of spatial statistics. For example, a well-known difficulty in the interpretation of moments is the possibility that they may exist at a point that has no observations. Thus the first moment can, as in a normal distribution, be coincident with the modal value of the distribution, or, on the other hand,

occur at a point that is devoid of data. In either event, the moments always give the "balance point" of the distribution, and we therefore consider the moments to be valid indicators of the distribution of events in space, especially when the moments are considered in the context of the distribution from which the moments are computed.

We wish to emphasize also that the spatial statistics discussed in this paper should not be construed as estimates of the parameters of a bivariate normal distribution, but rather as indices of spatial central tendency, dispersion, and orientation. To emphasize our point we compare some typical examples of spatial statistics for effort and CPUE with corresponding marginal normal distributions that have the same parameter values as the spatial statistics. These typical examples show the marginal distribution of effort and CPUE for January 1957 (fig. 7). From these we can see that the first moment is a reasonable indicator of a modal value for CPUE and longitudinal effort, but that the latitudinal moment for effort lies between the equatorial and North Pacific fishing grounds. The latitudinal distribution of CPUE tends to be more concentrated than if it corresponded to a normal distribution. The longitudinal CPUE and effort tend to be less concentrated than a corresponding normal distribution. The latitudinal distribution of effort is, however, a special case, since it clearly represents

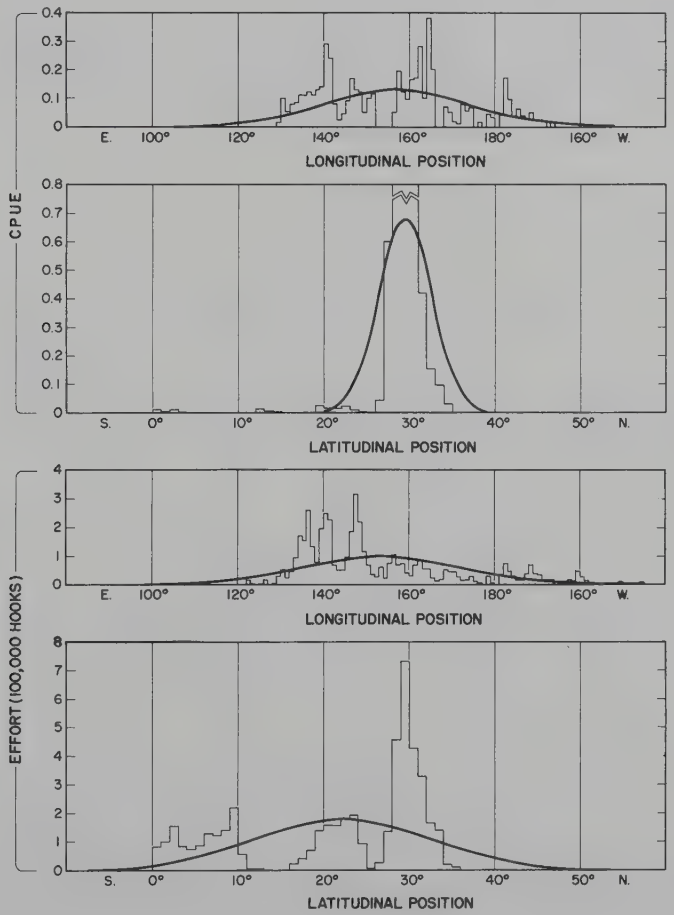

Figure 7.--Relation between spatial statistics (January 1957) and normal probability distribution for effort and CPUE (in numbers of fish per hundred hooks).

two fishing grounds, a northern fishing ground and an equatorial ground, and thus the latitudinal first moment of effort gives a better representation of the balance between the two grounds, rather than the central tendency of either.

Periodicities and Trends

Periodicities and trends in spatial statistics can be evaluated from time series plots of these statistics. Figures 8, 9, and 10 show spatial statistics for each month and year for effort, catch, and CPUE. They also show the values for the peak months. The figures illustrate the presence of annual periodicities as well as longer term trends. The annual periodicities are summarized in table 3, which gives the frequency by months of maximum and minimum values of each spatial statistic for effort, catch, and CPUE.

The long-term trends of the spatial statistics are indexed by the February values. Use of February values is justified by the relatively high within-year correlation among the points for each statistic in any year. The trends are interpreted from the slopes of least-square regression lines fitted to the data (figs. 11-13). A discussion of the annual periodicities and longer term trends for effort, catch, and CPUE follows.

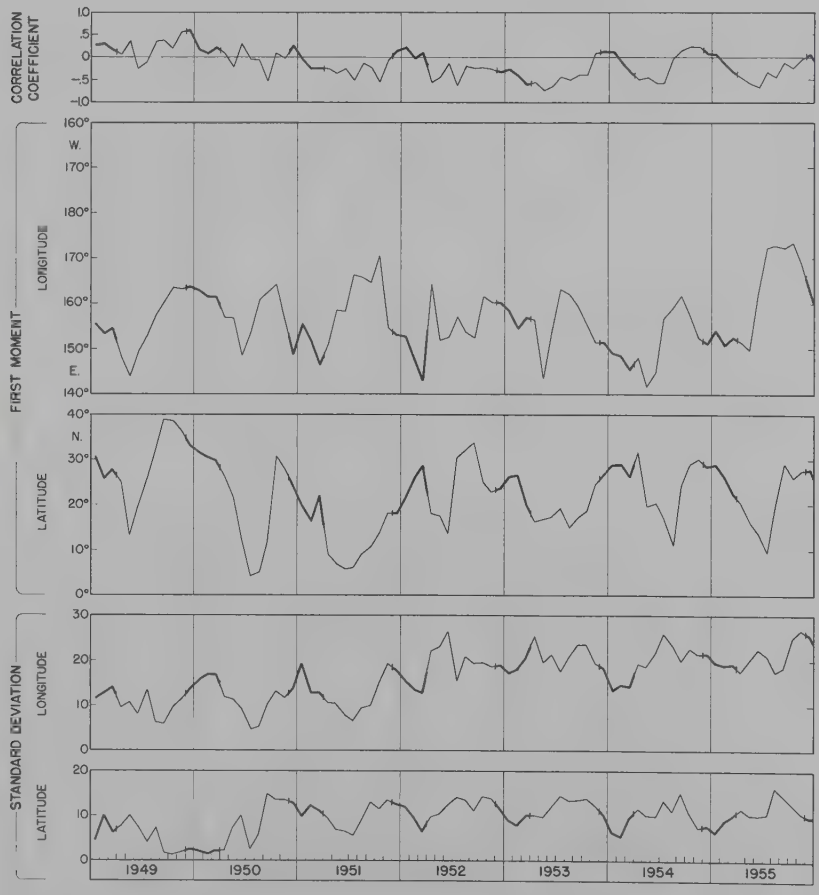

Figure 8.--Spatial statistics for effort 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.

Effort.--Referring to table 3, the maximum longitudinal first moment (eastwardmost extension) of effort occurred in July through October. The minimum longitudinal first moment (westwardmost extension) came in March through June. The maximum latitudinal moment (northernmost extension) was most often in September, October, and November although this maximum did occur in March and April. All months except August, September, and December showed a maximum longitudinal standard deviation and the minimum longitudinal standard deviation occurred in January through April and also in July. The latitudinal standard deviation of effort attained maximum values mostly in the third quarter--July, August, and September--whereas the values were minimum in the first quarter, in June and July, and in October. The correlation coefficient was at a maximum in November, December, and January; it was at a minimum in March through July and also in September.

From figure 8 we can see the relation between the spatial statistics for effort and the peak fishing periods. The longitudinal moment is generally at a minimum value during the peak fishing period. The latitudinal moment tends to be near its maximum value at the beginning of the peak period and tends to decline through the peak period. Both the latitudinal

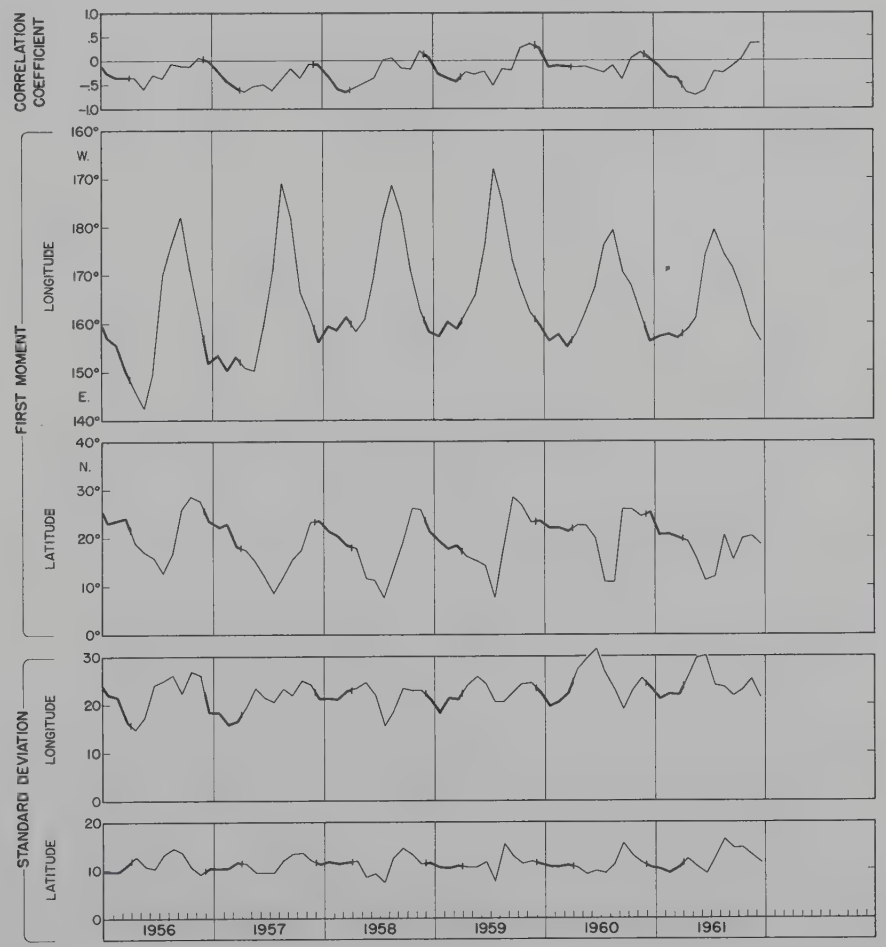

Figure 8.--Spatial statistics for effort 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.--Continued.

and the longitudinal standard deviations exhibit relative or absolute minima during the peak periods. The correlation coefficient for effort is similar to the latitudinal moment in that it tends to be near a maximum at the beginning of a peak period and then declines throughout the peak period.

The longer term trends in effort are shown in figure 11. The longitudinal moment tends to move toward the east, on the average, 0.42 degree (about 25 miles or 46 km.) per year. The latitudinal moment tends to move toward the south, 0.52 degree (about 31 miles or 57 km.) per year. The longitudinal standard deviation tends to increase 0.75 degree (about 45 miles or 83 km.) per year whereas the latitudinal standard deviation increases at the lesser rate of 0.27 degree (about 16 miles or 30 km.) per year. The correlation coefficient decreases, on the average, from a value of near 0 to nearly -0.4 over the 13-year period.

Catch and catch-per-unit-of-effort.--The spatial statistics for catch and CPUE are, in general, similar and therefore do not warrant separate discussion.

Again referring to table 3 and to figures 9 and 10, we see that the maximum longitudinal moments for catch and CPUE are centered on the third quarter of the year whereas the most typical time for the minimal value for the lon-

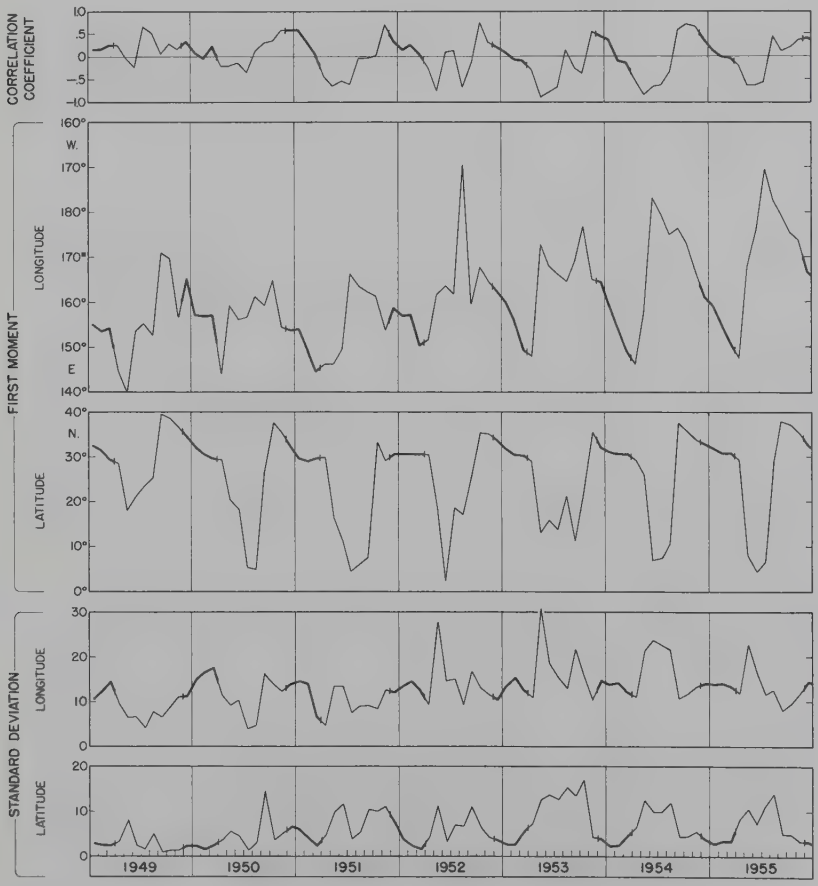

Figure 9.--Spatial statistics for catch 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.

gitudinal moments occurs during the beginning of the second quarter of the year. The latitudinal moments usually have their maximum values in September or October and their minimum values in the second or third quarter. The maximum longitudinal standard deviations occur mostly in the second quarter whereas values tend to be minimal in March or April or several months later, in the third or fourth quarter of the year. The latitudinal standard deviations exhibit maximum values most frequently in the third quarter, and their minimal values most typically are in the first quarter. The correlation coefficient has its maximal values in the latter half of the year; most minimal values occur during the second quarter.

Returning to figures 9 and 10, we can see the relation of the spatial statistics for catch and CPUE to the peak fishing period. The pattern they exhibit is remarkably consistent among the 13 years for which we have data. The longitudinal moment, for example, declines throughout the peak period and reaches its minimum value at or near the end of that period. The peak period appears to be superimposed on the latter portion of a net westward movement of the longitudinal moments. Similarly the latitudinal moment for both catch and CPUE exhibit a net decline throughout the peak period; the rate of decline of the latitudinal moments, however,

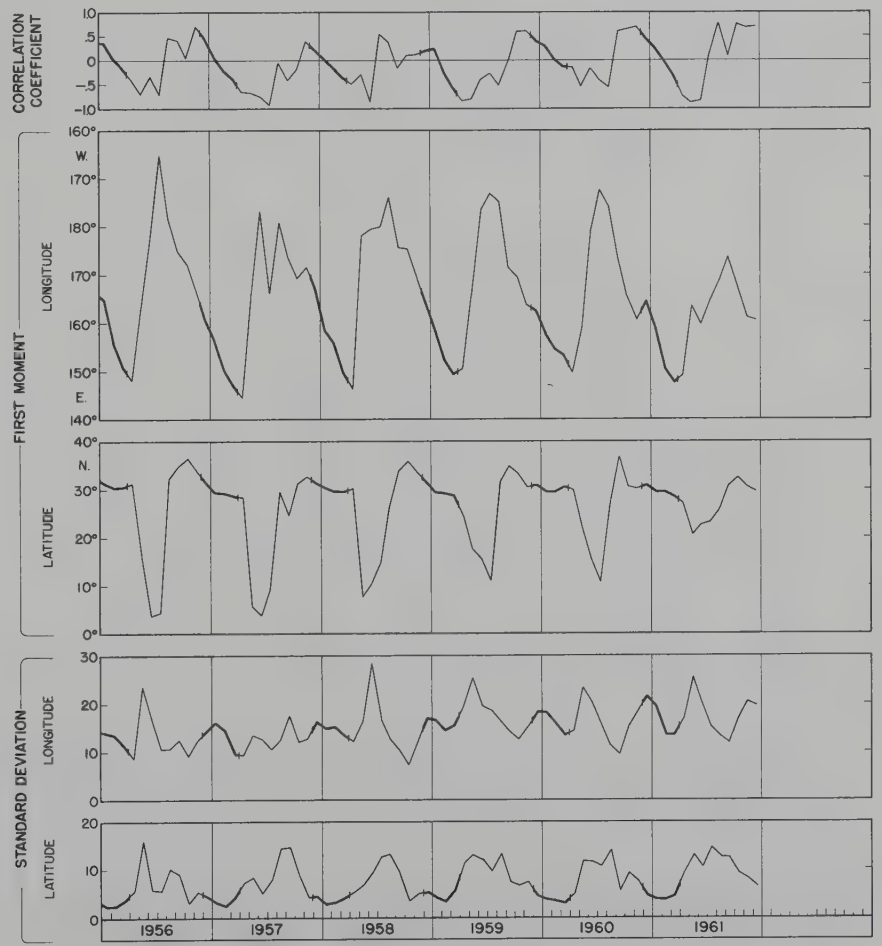

Figure 9.--Spatial statistics for catch 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.--Continued.

tends to decrease, or even, on occasion, to increase during the last few months of the peak period. The longitudinal standard deviations exhibit a maximum value while the latitudinal standard deviations tend to exhibit minimal values during the peak period. Thus, during the peak fishing season the catch and CPUE exhibit, simultaneously, a maximum latitudinal contraction and maximum longitudinal expansion. The correlation coefficients of both catch and CPUE decline throughout the peak periods.

The longer term trends based on the February index for catch and CPUE are shown in figures 12 and 13. The 1949 intercept for the longitudinal moment of catch is long. 154.9° E., and that for CPUE is also long. 154.9° E. Over the 13-year period the catch tends to move toward the west at a faster rate than the CPUE (0.69 degree or about 41 miles or 76 km. per year versus 0.17 degree or about 10 miles or 19 km. per year). The intercepts for the latitudinal moments are lat. 30.6° N. for catch and lat. 30.8° N. for the CPUE. The CPUE tends to move to the south at a greater rate--0.13 degree (about 8 miles or 15 km.) per year--than the corresponding index for catch, which moves south at only 0.08 degree (about 5 miles or 9 km.) per year. The 1949 intercept for the longitudinal standard deviation of catch is 14.9 degrees, whereas that for CPUE is 14.3 degrees.

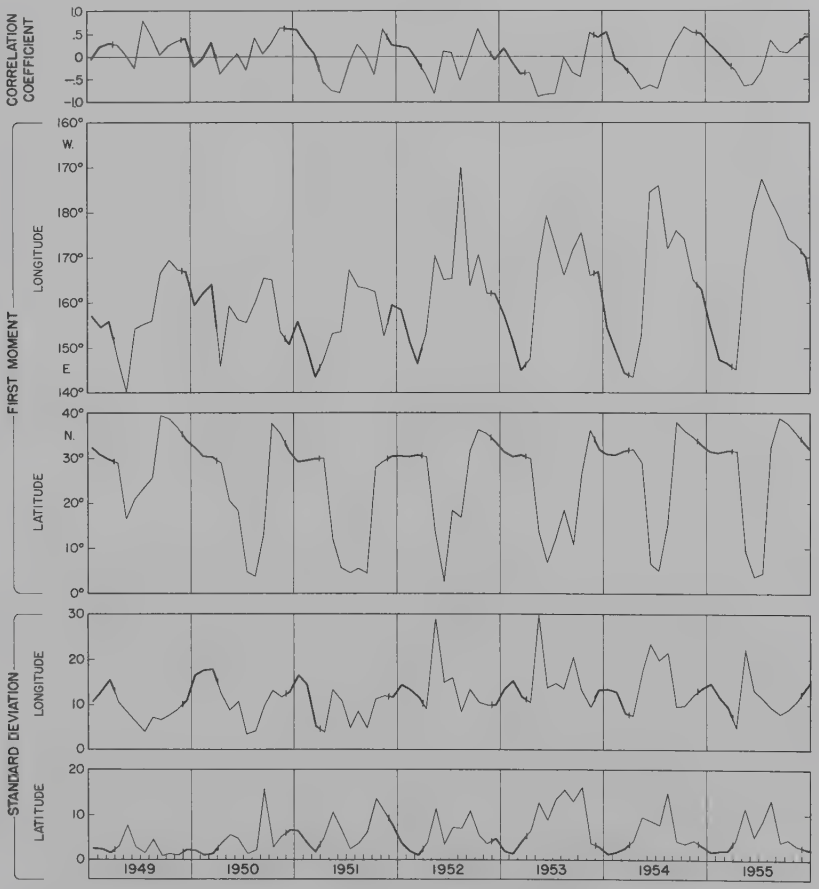

Figure 10.--Spatial statistics for CPUE 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.

The longitudinal standard deviation of catch tends to decrease at a rate of 0.27 degree (16 miles or 30 km.) per year, whereas that for CPUE tends to increase, slightly, at a rate of 0.04 degree per year. The latitudinal standard deviation of catch has an intercept of 1.93 degrees (about 114 miles or 211 km.) and increases at a rate of 0.01 degree (about 1 mile or 2 km.) per year, whereas the latitudinal standard deviation of CPUE has an intercept of 2.29 degrees (about 137 miles or 254 km.) and increases at a rate of 0.11 degree (about 7 miles or 13 km.) per year. The correlation coefficient indicates that the distributions of both catch and CPUE are oriented, slightly, in a northeast-southwest direction in 1949; rotate to an east-west orientation in 1955; and after 1955 continue to rotate in a clockwise direction toward a northwest-southeast orientation.

Average Location

This section considers the average location of effort and albacore CPUE inferred from averages of the CPUE and effort first-order spatial statistics for each month. Figures 14 and 15 show the average positions of the first moments of effort and CPUE for each month. The average CPUE moment (fig. 14) is located at long. 164° E., lat. 33° N. in November and moves south and west to long. 147° E., lat. 29°

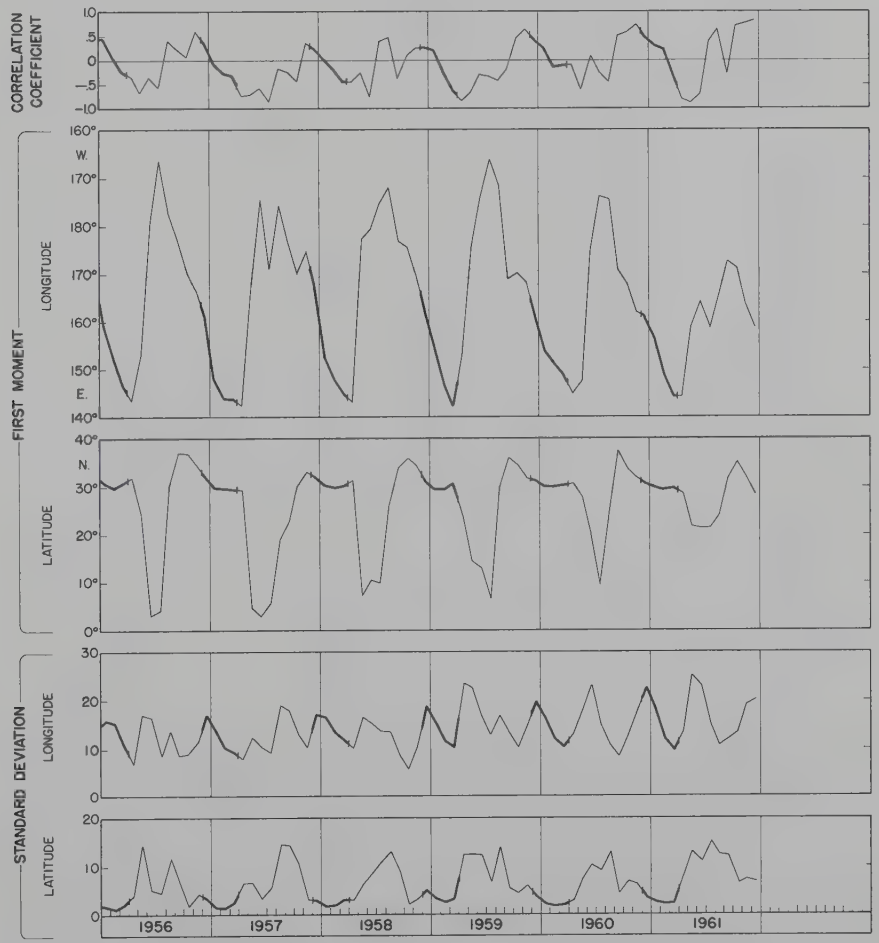

Figure 10.--Spatial statistics for CPUE 1949-61 on the North Pacific albacore longline grounds. The heavy line represents the peak fishing period from December to March.--Continued.

Table 3.--Frequency of maximum and minimum values of moments, standard deviations, and correlation coefficients for effort, catch, and CPUE for each month during the 1949-61 period

Variable and quarter of year	Month	First moment				Standard deviation				ρ	
		Long.		Lat.		Long.		Lat.		Max.	Min.
		Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.		
Effort											
I	January	-	-	-	-	1	4	-	2	3	-
	February	-	-	-	-	1	1	-	2	-	-
	March	-	5	1	-	1	1	-	1	-	1
II	April	-	1	1	-	1	2	-	-	-	1
	May	-	6	-	1	2	-	1	-	-	3
	June	-	1	-	3	2	-	-	1	-	2
III	July	3	-	-	7	2	3	3	6	-	4
	August	3	-	-	2	-	-	3	-	-	-
	September	2	-	6	-	-	2	5	-	-	2
IV	October	5	-	2	-	2	-	-	1	-	-
	November	-	-	2	-	1	-	1	-	4	-
	December	-	-	-	-	-	-	-	-	6	-
Catch											
I	January	-	-	-	-	2	-	-	2	-	-
	February	-	-	-	-	-	-	-	7	-	-
	March	-	5	-	-	2	1	-	2	-	-
II	April	-	7	-	-	1	5	-	-	-	2
	May	-	1	-	2	4	-	2	-	-	7
	June	2	-	-	6	3	-	-	-	-	3
III	July	6	-	-	3	-	2	1	1	1	1
	August	2	-	-	1	1	1	6	-	1	-
	September	1	-	6	1	-	1	2	1	-	-
IV	October	2	-	4	-	-	2	2	-	2	-
	November	-	-	2	-	-	1	-	-	7	-
	December	-	-	1	-	-	-	-	-	2	-
CPUE											
I	January	-	-	-	-	-	-	-	5	-	-
	February	-	-	-	-	1	-	-	3	-	-
	March	-	4	-	-	2	-	-	3	-	-
II	April	-	8	-	-	-	5	-	-	-	1
	May	-	1	-	2	7	-	4	-	-	8
	June	2	-	-	5	2	-	1	-	-	2
III	July	5	-	-	4	-	2	1	1	2	2
	August	2	-	1	1	-	-	4	-	1	-
	September	2	-	4	1	1	4	2	1	-	-
IV	October	2	-	6	-	-	2	1	-	3	-
	November	-	-	2	-	-	-	-	-	6	-
	December	-	-	-	-	-	-	-	-	1	-

N. by April. In figure 15 we can see that the center of effort is located at long. 160° E., lat. 26° N. in November and moves south and west to long. 155° E., lat. 19° N. in April. The center of effort is to the west of CPUE in November, but by April the center of effort is to the east of the CPUE. Latitudinally, however, the relative positions of CPUE and effort are stable; the centroid of effort is always several degrees to the south of CPUE. Thus, the distribution of effort is not centered on apparent abundance.

The striking feature of figure 14 is that there is only a slight variation (for fishery data) of the observed points around the general mean. This consistency is especially striking when one considers that the moment could be distributed over a much larger area of ocean. The low variability in the distribution of the CPUE data suggests that highly accurate predictions could be made for the location of apparent abundance of albacore during the peak months by the use of only the data in figure 14.

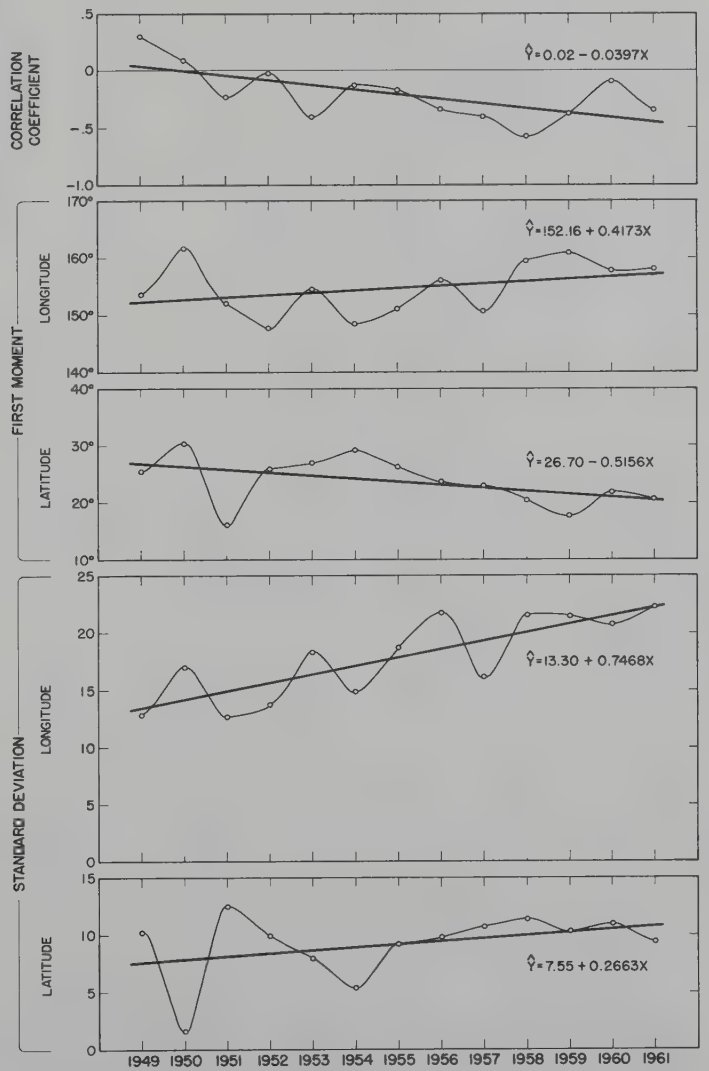

Figure 11.--Trends in February effort spatial statistics.

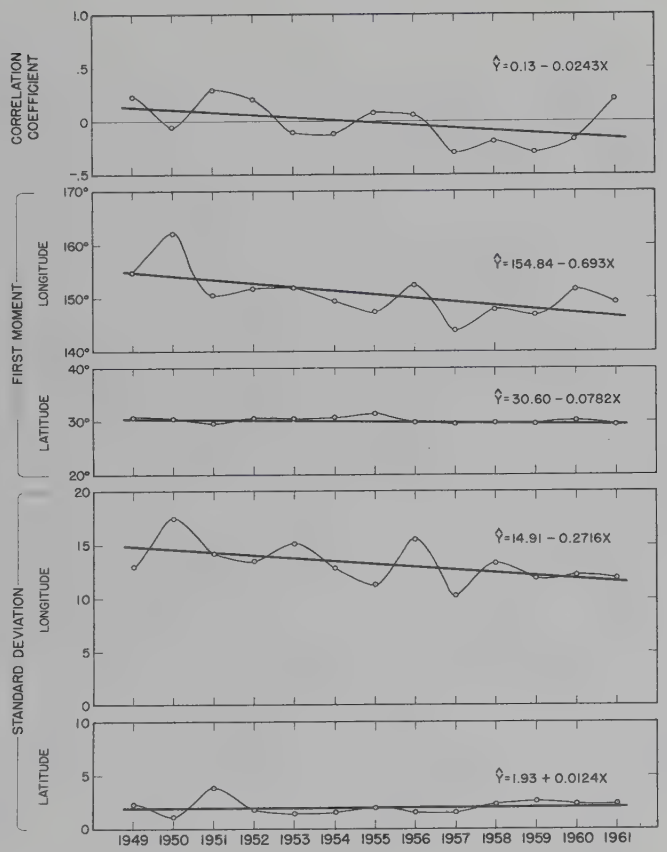

Figure 12.--Trends in February catch spatial statistics.

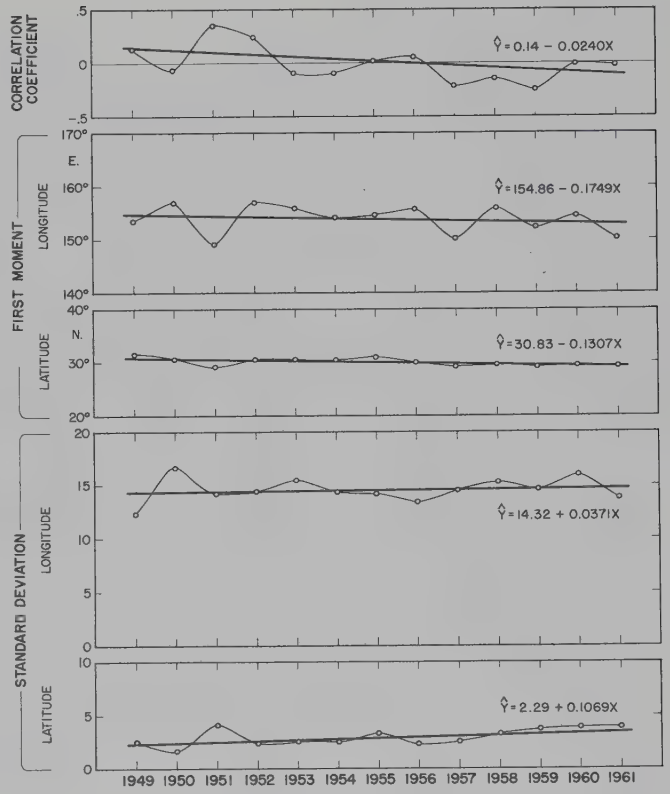

Figure 13.--Trends in February CPUE spatial statistics.

Despite the low variability about the general mean of CPUE, we examined the data to determine whether the monthly means for 6 peak months (October-March) for some years were consistently north or south, or, east or west of the overall mean. This determination was made by counting for each year the number of months that were to the east of the mean and the number west of the mean. We used a similar procedure to compare, for each year, the number of monthly means to the north and the number of monthly means to the south of the general mean. These enumerations are set forth in table 4. First, with respect to the east-west comparisons, we note that the χ^2 test for homogeneity was nonsignificant (χ^2 = 20.2, 12 d.f.). As a result the data were pooled, yielding a χ^2 of 0.32 (1 d.f.), which is also not significant and suggests that there is no evidence to indicate a consistent pattern for most months, in any year, to be to the east or west of the overall mean. For the north-south com-

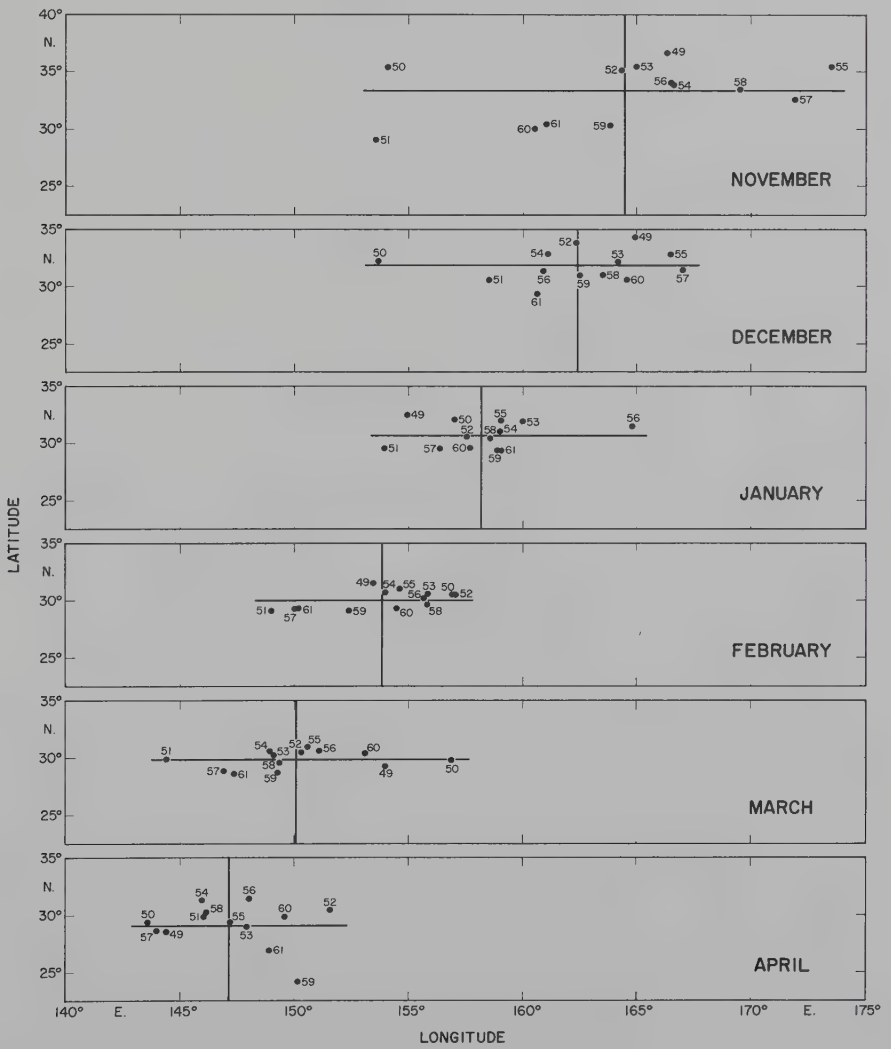

Figure 14.--Latitudinal and longitudinal moments of CPUE for each month and year. The center of the cross represents the average position of the latitudinal and longitudinal moments for each month.

parisons, however, the χ^2 test for homogeneity was significant (χ^2 = 45.1, 12 d.f.); thus, individual χ^2 for the north-south comparisons showed that 1954 and 1955 had a significant number of means to the north of the general mean, but in contrast 1959 and 1961 had a significant number of means to the south of the general mean.

Apparent Movement

The relatively stable periodicity in the CPUE spatial statistics suggested the possibility of computing the velocity of the two-dimensional first moment as it moves through space. We call the movement deduced from this velocity apparent movement because it could result from several modes of actual movement. For

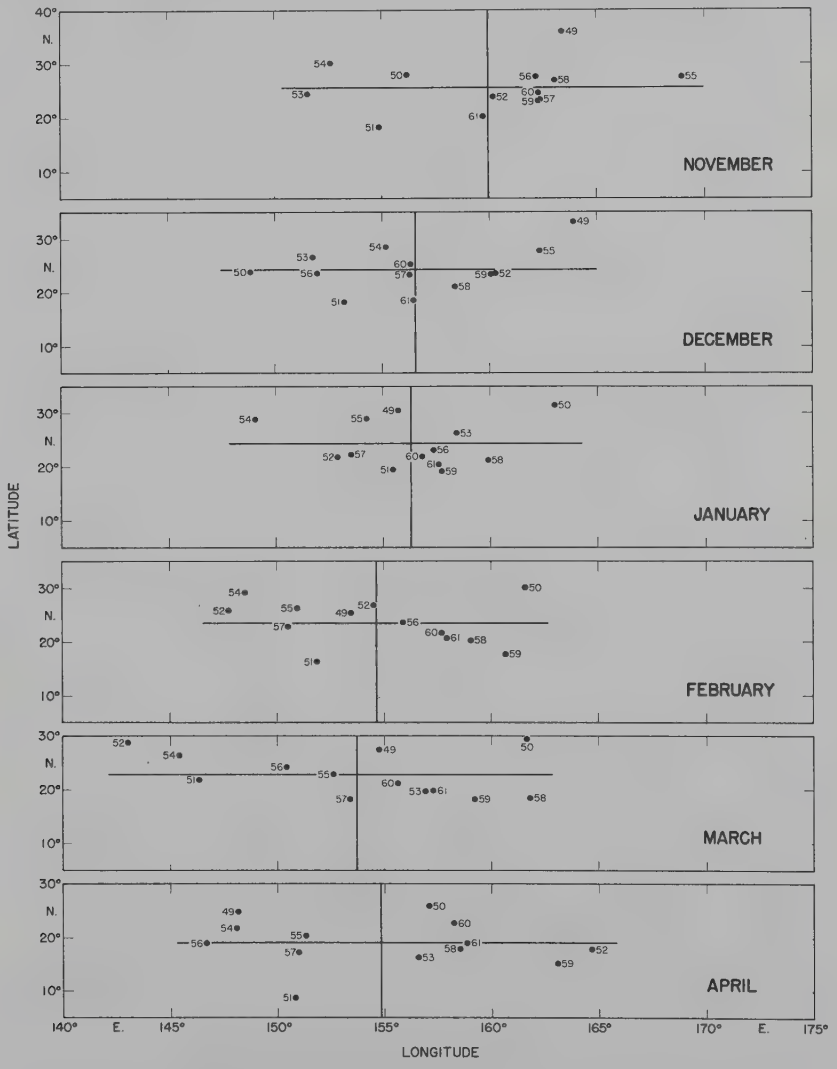

Figure 15.--Latitudinal and longitudinal moments of effort for each month and year. The center of the cross represents the average position of the latitudinal and longitudinal moments for each month.

Table 4.--Number of months (October-March) that the two-dimensional first moment was either to the north or south, or east or west of the general mean position and χ^2 tests of significance

Year	West	East	χ^2	North	South	χ^2
	Month			Month		
1949	3	3	0.00	4	2	0.66
1950	4	2	0.66	5	1	2.66
1951	6	0	6.00*	1	5	2.66
1952	3	3	0.00	5	1	2.66
1953	1	5	2.66	5	1	2.66
1954	3	3	0.00	6	0	6.00*
1955	0	6	6.00*	6	0	6.00*
1956	1	5	2.66	5	1	2.66
1957	4	2	0.66	0	6	6.00*
1958	2	4	0.66	2	4	0.66
1959	3	3	0.00	0	6	6.00*
1960	2	4	0.66	2	4	0.66
1961	4	2	0.66	0	6	6.00*
Homogeneity χ^2			20.2 not significant			45.1*
χ^2 on totals			0.32 not significant			-

example, (1) the albacore might actually swim at the same velocity as that observed for the first moment; (2) the net distance moved by the albacore might be close to zero even though the CPUE first moments exhibit movements in time--the observed apparent movement being induced by a temporally and spatially variable field of catchability coefficients over the fishing ground; (3) the albacore might tend to be constrained to a horizontal lamina of ocean, swim in this lamina in a sinusoidal pattern, and travel greater distances and consequently at greater velocities than would be deduced from computing this velocity from initial and terminal positions; (4) exactly the same situation as in (3) except that the fish might be constrained to move in a vertical rather than in a horizontal lamina; and as a final example (5) the albacore might be constrained to move back and forth over a straight line traversing distances that are greater than those implied by the motion of the moments. At the present stage of our knowledge, the mode or combination of modes of movement that actually apply to the albacore is difficult to deduce.

The average rate of apparent movement for the peak midwinter fishing period was computed for both the longitudinal and latitudinal directions. We computed the longitudinal velocity by subtracting the longitudinal moment at the end of March from the longitudinal moment at the beginning of December. The difference in degrees of longitude was converted to miles and divided by the number of days (120) to obtain the average longitudinal movement per day. The average latitudinal movement per day was computed in a similar fashion.

The average longitudinal movement per day is 6.25 miles (11.58 km.), and the average latitudinal movement per day is 1.65 miles (3.05 km.), giving a resultant velocity of about 6.5 miles (12.04 km.) day^{-1} (table 5). A slight increase in longitudinal velocity appears over the years, since the velocities for the first 3 years (1950, 1951, 1952) are less than the average velocity of 6.25 miles (11.58 km.) day^{-1}; all the other velocities are greater than the average velocity except that for 1960.

Relating the velocity of the moment to actual swimming speeds is rather difficult since there are not many critical studies of an average swimming speed for tunas at sea. Some detailed studies such as that by Yuen (1966) have shown that swimming speeds of feeding tunas (yellowfin tuna, Thunnus albacares, and skipjack tuna, Katsuwonus pelamis) are of the order of one body length per second. This would amount to 86 km. day^{-1}--a speed far in excess of 7 miles (13 km.) day^{-1}.

The cause of the discrepancy between the velocity of the albacore moments and the expected swimming velocity provides an interesting area of inquiry. It is well known that tunas swim continuously, probably in order to maintain a flow of water over the gills. The continuous swimming is necessary to provide the flow of water over the respiratory surfaces because tunas, unlike most fishes, have no musculature to pump water over the gills. Continuous swimming is facilitated by structural modifications that provide well-developed lifting surfaces such as the pectoral fin (Magnuson, 1970). The lifting surfaces help the tuna maintain hydrostatic equilibrium. The pectoral fin of the albacore is especially well developed, so the albacore may be able to swim at lower velocities than, say, the skipjack or the yellowfin tuna and still be able to maintain hydrostatic equilibrium. Thus the albacore might be adapted to a slower swimming speed than the other tunas. It is unlikely, however, that structural modification alone could account for the discrepancy between the velocity of apparent movement and the "potential" swimming velocity.

Another possibility is that tuna soar like birds (Cone, 1962) utilizing the energy in ver-

Table 5.--Position of longitudinal and latitudinal first moments at the beginning of December and at the end of March for each year during the study period. The average movement per day was calculated by converting the December-March differences into miles and dividing by 120

Year	Position		Longitudinal movement		Position		Latitudinal movement	
	Dec.	Mar.			Dec.	Mar.		
	Long. ° E.		Miles day^{-1}	(km.)	Lat. ° N.		Miles day^{-1}	(km.)
1950	160.0	150.0	4.35	(8.06)	35.5	29.7	2.90	(5.37)
1951	154.0	145.4	3.74	(6.93)	33.8	29.9	1.95	(3.61)
1952	156.0	151.0	2.18	(4.04)	30.0	30.5	-0.25	(-0.46)
1953	163.5	148.5	6.53	(12.10)	34.7	29.8	2.45	(4.54)
1954	170.0	149.0	7.49	(13.88)	33.5	31.0	1.25	(2.32)
1955	163.5	149.0	6.31	(11.69)	33.3	30.1	1.60	(2.97)
1956	170.0	149.6	8.88	(16.46)	34.4	31.0	1.70	(3.15)
1957	163.5	145.5	7.83	(14.51)	32.8	28.6	2.10	(3.89)
1958	169.3	148.1	9.23	(17.10)	32.0	29.9	1.05	(1.95)
1959	166.5	149.9	7.22	(13.38)	32.7	26.1	3.30	(6.12)
1960	163.0	151.7	4.92	(9.12)	30.8	30.1	0.35	(0.65)
1961	162.5	148.0	6.31	(11.69)	30.5	27.8	1.35	(2.50)
Average			6.25	(11.58)			1.65	(3.06)

Resultant = $\sqrt{(1.65)^2 + (6.25)^2}$ = 6.46 miles (11.97 km.) day^{-1}

tical motions of their environmental medium to maintain equilibrium and thus do not need to sustain a continual threshold velocity to avoid sinking. We felt that some of these possibilities could be explored by studying the apparent velocities of the tagged fish reported by Otsu and Uchida (1963). Accordingly, we have plotted distance between the location of marking and recapture for the albacore tagging data summarized by these authors as a function of time at liberty (fig. 16). We can see from these data that the points fall into essentially two groups. The first is a group of relatively short-term recoveries (time at liberty $<$ 100 days), and the second is a group of relatively long-term recoveries (time at liberty $>$ 200 days). The latter group shows that there is a tendency for the fish that are at liberty the longest to be recaptured nearer to the site of tagging. We interpret this tendency to reflect a circulation pattern of the albacore in the North Pacific; hence low velocities as deduced from the distance traveled by tagged fish could result from the fish actually moving a short distance or this returning of the fish to the site of tagging after a sojourn to some other area. We should be cautious, therefore, in interpreting any but the maximal velocities as actual swimming speeds. These maximal velocities in the tagging data are about 15 miles (28 km.) day^{-1}, a velocity which is about double that deduced from the moments. We conclude that if the inferred transpacific velocity of albacore from tagging studies is equivalent to the velocity of the albacore on the longline grounds, as inferred from the motion of the moments (under the assumption that apparent movement is equivalent to actual movement), then the albacore are, on the average, constrained to move each day within an area circumscribed by two intersecting lines; the length of each being 15 miles (28 km.) and the distance between the intersections being 7 miles (13 km.). A considerable discrepance, between 15 miles (28 km.) day^{-1} and 86 km. day^{-1}, still remains. We conclude that the most likely cause for this discrepance is that the albacore generally follow tortuous routes between any two, even closely spaced points. If tunas actually do soar in the same fashion as the birds studied by Cone (1962), then perhaps they also follow the trochoidal path described by Cone. Such a path would account for a considerable difference between a velocity on a straight line connecting a starting point and a terminal point and a velocity computed on the actual nonlinear path between the two points. A nonlinear path is very likely considering that a tuna in some fixed time must swim a considerable distance to maintain hydrostatic equilibrium, especially

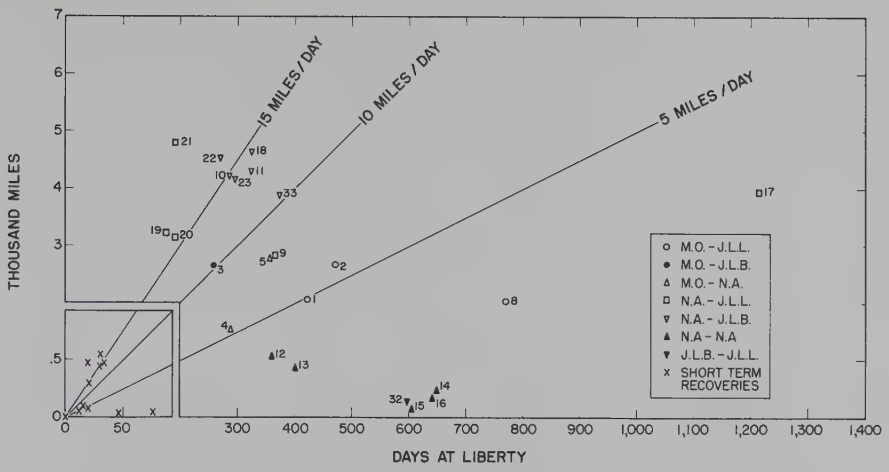

Figure 16.--Distance from site of tagging as a function of time at liberty. Note that the shorter term recoveries are plotted on an expanded scale. Data are from Otsu and Uchida (1963). (15 miles = 27.8 km., 10 miles = 18.5 km., 5 miles = 9.3 km.)

if it were not capable of soaring, and the fact that tagged tunas have been known to be captured at essentially the same location as that in which they were tagged after several weeks at liberty. Since our considerations are restricted mostly to "apparent" movement, our conclusions relative to the actual movements of the albacore are of course, to a large extent, speculative.

MIGRATORY ROUTE

An understanding of yield-per-recruit and other dynamical problems relevant to the albacore on the North Pacific longline grounds depends, to a large extent, on an understanding of the nature of albacore immigrations and emigrations from the various fisheries in the North Pacific Ocean. Models describing these immigrations and emigrations have been forwarded in the literature. In this section we review these models in relation to our study of the spatial statistics.

Our present understanding of the migration of albacore over the entire North Pacific Ocean is essentially based on the work of Clemens (1961, 1963) and Otsu and Uchida (1963). The model formulated by Clemens established the relationship between those albacore taken in the coastal waters of North America and those taken by the Japanese fisheries of the North Pacific. According to Clemens the albacore are first recruited to the North American fishery off the coast of California, move north along the coast and then west, continuing along the subtropical convergence until they encounter the Japanese fisheries. The model proposed by Otsu and Uchida (subsumed in figure 9 of their paper and reproduced here as fig. 17) is in many respects similar to that of Clemens, but is more explicit in describing the clockwise as well as the more typical counterclockwise movements and postulating a definite pattern of the mode of entrance of the North American escapement into the Japanese fisheries: viz, from North American, to longline, to pole and line.

The evidence presented by Otsu and Uchida and by Clemens clearly confirms that at least the majority of albacore taken in the Japanese fishery are emigrants from the North American fishery. It is not clear, however, that the albacore move directly from the North American to the longline and then to the pole-and-line fishery. We believe, rather, that a large proportion of the albacore that emigrate from the North American fishery first enter the pole-and-line fishery (we emphasize that our inferences with respect to movement are fishery-specific and therefore our statement that the albacore "first enter the pole-and-line fishery" does not preclude the possibility that

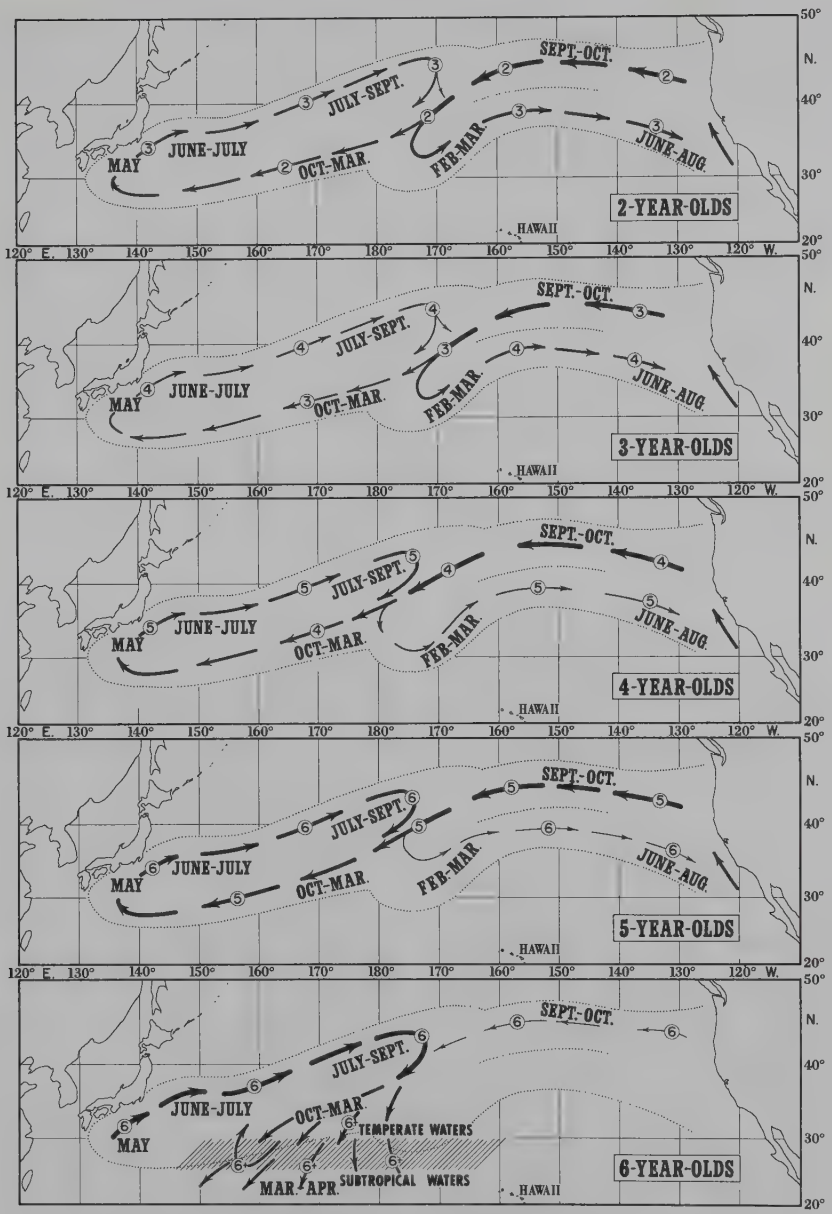

Figure 17.--Model of albacore migrations in the North Pacific Ocean, by age groups (ages encircled) taken from figure 9 of Otsu and Uchida (1963).

albacore swim through the area of the longline fishery, but are, for the most part, not vulnerable to capture). Our belief that a large proportion of the albacore that emigrate from the North American fishery first enter the pole-and-line fishery is based on several lines of evidence: (1) size distribution, (2) size distribution combined with estimates of growth rate and the time interval between middates for the various fisheries, (3) the correlation between apparent abundance in the longline fishery and in the pole-and-line fishery, and (4) tagging data.

Size Distribution

We note that the average size of the albacore taken in the pole-and-line fishery is consistently less than the average size of albacore taken in the longline fishery (fig. 5). The difference in size implies that the fish in the longline fishery are, on the average, older than the fish in the pole-and-line fishery. This difference by itself might be taken to indicate that the albacore enter the longline fishery only after passing through the pole-and-line fishery. Two qualifications to this interpretation are necessary. First, young albacore are taken along the Japanese coast (see, for example, Otsu and Uchida, 1963). It is unlikely these young albacore are emigrants from the North American fishery. They are probably recruited directly into Japanese coastal waters from the place of their birth, probably the equatorial western Pacific. If the eastern Pacific emigrants were partitioned equally between the pole-and-line and the longline fishery then, ceteris paribus, the average length of the albacore in the two fisheries would be roughly equal (actually the albacore taken by the longline fishery would be slightly smaller than the albacore taken by the pole-and-line fishery, owing to the temporal difference in the peak fishing period). But if young albacore, directly from the spawning grounds, were taken in the pole-and-line catch then the average length of the pole-and-line fish would be less than that of the fish on the longline grounds. Thus, the observed difference in average size between the fish taken on the longline grounds and the pole-and-line grounds may be the result of the pole-and-line fishery's having a significant recruitment of young, small fish that have never passed through the eastern Pacific fishery. Our opinion, however, based on examination of length frequencies given by Suda (1963a), is that the influence of recruitment directly from the spawning grounds has a negligible effect on the difference between the average lengths of the longline fish and the pole-and-line fish. A second point is that the discrepance in average length between the fish in the two fisheries should not preclude an interpretation that some of the albacore may be captured in the longline fishery before reaching the pole-and-line fishery. Clearly the difference in average age of the fish in the two fisheries is a function of, among other things, the proportion of fish that enter either fishery.

Size Distributions, Growth Rate, and the Time Interval Between the Middates of the Various Fisheries

The California fishery is centered on mid-August (for timing of the various fisheries we use data from Suda (1963b)), and the modal size of fish taken in this fishery appears to be about 65 cm. (Clemens and Craig, 1965). The longline fishery peaks 5 months after the California fishery at the end of January, and the pole-and-line fishery peaks about 4 months after the longline fishery, at the end of May. If we use the VBGF (von Bertalanffy growth function) for albacore computed by Shomura (1966) with Otsu's (1960) data as having parameters $L_\infty = 119$, $K = 0.25$, then the 65 cm. albacore would be 74 cm. after 5 months and 78 cm. after an additional 4 months. Thus, if the albacore simply moved from coastal North America to the longline grounds, to the pole-and-line grounds, then we should expect that the fish in each fishery should have modal lengths of 65 cm., 74 cm., and 78 cm., respectively. This expectation is not met, however, because the data given by Suda (1963a) show that the albacore taken in the pole-and-line fishery average several centimeters smaller than those taken in the longline fishery. This difference suggests considering an alternative, viz, that the albacore move from the coastal North American fishery to the pole-and-line fishery to the longline fishery. If the predominant movement was indeed from the North American, to the pole-and-line, to the longline fisheries, then the 65 cm. fish would, according to the same VBGF as before, appear as 78 cm. fish 9 months later in the Japanese pole-and-line fishery and as 85 cm. fish in the Japanese longline fishery 8 months after appearing in the Japanese pole-and-line fishery. An average size of 78 cm. in the pole-and-line fishery and of 85 cm. in the longline fishery is

in good correspondence with the average sizes of the fish (fig. 5) taken in these fisheries and therefore suggests that, as outlined in figure 18, the North American to pole-and-line to longline route is more likely than the North America to longline to pole-and-line route.

Correlation Between Apparent Abundances for the Pole-and-line Fishery and for the Longline Fishery

A third line of evidence that bears on the route of the albacore is that presented by Suda (1958 and 1963b). First, he computed the correlation between the apparent abundance for each pole-and-line fishing season and the apparent abundance for each subsequent longline fishing season. Second, he computed the correlation between the apparent abundance for each pole-and-line fishing season and the apparent abundance for each preceding longline fishing season. He found a much higher correlation coefficient between pole-and-line apparent abundance and apparent abundance in the subsequent longline season than that between the pole-and-line apparent abundance and that of the preceding longline season. This result implies that the fish tend to move from the pole-and-line fishery to the longline fishery, rather than from the longline fishery to the pole-and-line fishery. A few points of caution should be mentioned, however, in considering these correlations. First, rather few degrees of freedom were available for computation of the correlation coefficients. Secondly, an examination of the scatter diagrams (Suda, 1963b) from which these correlations were computed shows that the poor correlation between apparent abundance for the pole-and-line season and the preceding longline season is generated, to a large extent, by a single datum. We note, also, that on the basis of the temporal occurrence of the pole-and-line and longline fisheries that we should a priori expect a higher correlation between the pole-and-line fishery and the preceding longline fishery than between the pole-and-line and subsequent longline fishery. This is because the midpoint of the pole-and-line fishery occurs only about 4 months after the midpoint of the longline fishery, whereas the middate of the longline fishery comes about 8 months after the middate of the pole-and-line fishery. Our a priori expectations are, however, not borne out, and thus we give greater weight to the interpretation that the predominant flow of albacore is from the pole-and-line fishery to the longline fishery.

Tagging Data

The last line of evidence is based on the tagging data presented in figure 16. We note from figure 16 that of the 11 fish tagged in the North American fishery 5 were recovered in the longline fishery and 6 were recovered in the pole-and-line fishery. Furthermore, we could interpret the data on the tagged fish that was at liberty 1,214 days to indicate that the fish passed through the pole-and-line fishery before entering the longline fishery. This assumption would imply that the pole-and-line fishery takes most fish that cross the Pacific at the time of the tagging experiment. Of the four fish tagged in midocean and recaptured, three were recovered in the longline fishery and one in the pole-and-line fishery. These recoveries

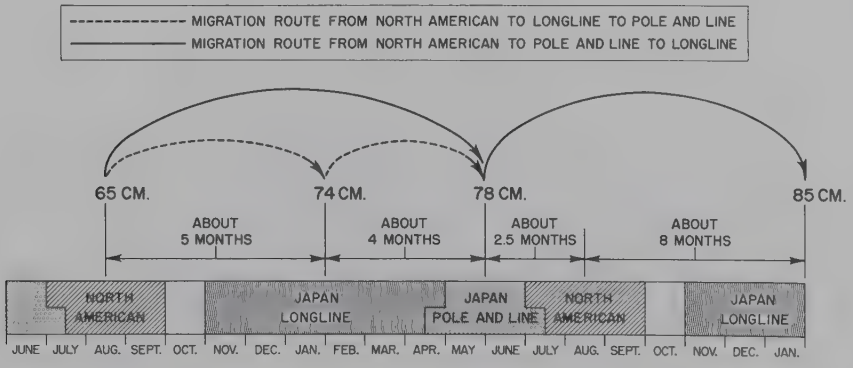
MIGRATION ROUTE FROM NORTH AMERICAN TO LONGLINE TO POLE AND LINE
MIGRATION ROUTE FROM NORTH AMERICAN TO POLE AND LINE TO LONGLINE
65 CM.
74 CM.
78 CM.
85 CM.
ABOUT 5 MONTHS
ABOUT 4 MONTHS
ABOUT 2.5 MONTHS
ABOUT 8 MONTHS
NORTH AMERICAN
JAPAN LONGLINE
JAPAN POLE AND LINE
NORTH AMERICAN
JAPAN LONGLINE
JUNE JULY AUG. SEPT. OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC. JAN.

Figure 18.--Expected lengths of albacore taking two different migration routes.

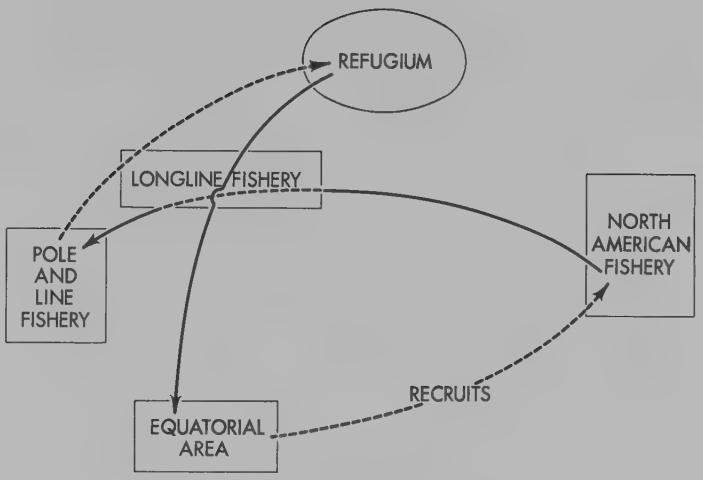

Figure 19.--Predominant movement of albacore in the North Pacific Ocean. Dashed lines passing through any block indicate relatively low vulnerability in that block, and solid lines through a block indicate high vulnerability. The position of the arrows should not necessarily be taken as the geographic location of the migration route.

might imply that most of the albacore in "mid-ocean" (a region that was essentially unfished for albacore) are taken in the longline fishery.

Thus, several lines of evidence suggest that after the albacore escape the North American fisheries, they first become vulnerable, in large quantities, to the Japanese pole-and-line fishery. The escapement from the pole-and-line fishery then provides a major source of fish for the Japanese North Pacific longline fishery. If we superimpose the movement pattern induced from our study of moments upon the larger pattern of predominant movement from North American to Japanese pole-and-line to Japanese longline fishery, we arrive at a more detailed model of albacore migration in the North Pacific than has heretofore been proposed. The movement pattern induced from moments is that the albacore move over the longline and pole-and-line grounds in a northeast to a southwest direction during the longline season and from a southwest to a northeast direction during the pole-and-line season. This feature of albacore apparent movement is well known (see Van Campen, 1960 and Suda, 1963b); the consistency of this movement in time and space, has, however, not been previously described. The results of applying the northeast to southwest movement during the longline season and the southwest to northeast movement during the pole-and-line season to the larger Pacificwide movement pattern suggest that after the albacore leave the North American fishery, they migrate through or near the Japanese longline grounds. (If the fish actually migrate through the longline grounds then their vulnerability to the longline gear is extremely low.) After passing the longline area the albacore enter the Japanese pole-and-line fishery about April. After being exposed to the pole-and-line fishery, the albacore migrate again through or, in some sense, proximal to the longline fishery, and again exhibiting little vulnerability to the longline gear. At this time their migration is in a southwest to northeast direction. After passing through or in proximity to the longline grounds the albacore spend about 10 months in a refugium (possibly the midocean area indicated by Otsu and Uchida), unavailable to capture, somewhere to the northeast of the longline grounds.[2] After a period of about 10 months the albacore move in a southwest direction through the longline fishery in which they exhibit maximum vulnerability to the longline gear. After escaping from the longline fishery the albacore proceed to the

[2]Indeed Koto (1963) shows that the albacore taken on the broadbill-swordfish longline grounds centered about lat. 10° N. of the albacore longline grounds as considered in this paper are, on the average, smaller than those taken on the longline grounds, which is consonant with the refugium concept. We should be cautious, however, because the difference in average length between the albacore taken on the albacore longline grounds and the albacore taken on the swordfish grounds might owe to a difference in the selectivity of swordfish gear which is fished nocturnally with a different hook suspension system and bait than that used for the albacore longline.

equatorial area. This hypothetical route of the albacore is shown schematically in figure 19.

DISCUSSION AND EVALUATION OF PRESENT UNDERSTANDING

Decline in Apparent Abundance

The apparent abundance of albacore on the North Pacific longline grounds exhibited a marked decline during the study period. The decline generates the question of the extent to which changes in actual abundance, changes in fishing intensity, or changes induced by the environment influenced the reduction in apparent abundance of albacore during the study period. Unfortunately, the appropriate data, customarily used for studies of this nature, were not available for the present investigation. As an example, estimates of nominal fishing effort would enable studies of the correlation between apparent abundance and fishing intensity. Suda (1963b: p. 1262) presents indices of fishing effort for albacore for each North Pacific longline fishing season (1951-59). His estimates are based on estimating the "number of standardized trips in North Pacific and other areas," and the ratio of number of trips in North Pacific to the number of standardized trips. Using these values Suda computed an index based on the ratio of the number of trips in the North Pacific to the number of trips standardized to a 1951 base of about 14,000 North Pacific trips. For an alternative estimate of effort on the albacore longline grounds, we have used Rothschild's (1966: pp. 96-99) estimates of the percent reported longline effort expended in each 20° quadrangle of the Pacific Ocean in 1953-61 and Otsu and Sumida's (1966) estimates of total Pacific Ocean longline effort for each year. We have applied Rothschild's percentages for quadrangles 9872 and 9873 (lat. 20°-40° N., long. 140° E.-180°) to Otsu and Sumida's estimates of total effort to arrive at an estimate in millions of hooks expended in the area lat. 20° to 40° N., long. 140° E. to 180°. These estimates in millions of hooks per year are: 1953, 7.2; 1954, 29.1; 1955, 27.2; 1956, 25.7; 1957, 13.3; 1958, 23.8; and 1959, 32.6.

The procedures used by Suda and us to estimate effort can be discussed from several points of view. Suda's is based on fishing effort applied to other species such as yellowfin or bigeye tuna. His computations are based on a trip as a unit of effort; the "trip" is a less fundamental unit of nominal effort for longline fishing than the "hook." His estimates of effort include fishing trips during the summer months when longline fishing for albacore in the North Pacific is essentially not prosecuted. Our estimates are based on a more restricted area than those of Suda but probably include some effort for bigeye and bluefin tunas. We have used the hook as a unit of nominal effort. Our estimates also include effort that is expended outside the peak fishing months, but since our area is restricted to the albacore grounds it is much less likely to include non-albacore effort even though data from the summer months are included in our computations. Unfortunately, our estimates of effort do not appear to be correlated with those given by Suda. Suda's estimates show a tendency for effort to decline during the 1951-59 period. Our estimates for the 1953-59 period do not exhibit a clear decline. Our CPUE index shows a negative correlation with our estimates of effort but not with Suda's estimates of effort. Since both estimates are derived through tortuous computations, it is difficult to determine, without additional detailed study, which is the better estimate.

The tentative nature of the estimates of effort creates difficulties in appraising the variables that influence the per-head rate of death. The conclusion that the per-head rate of death increases during the 1949-61 period essentially concurs with the studies of Suda that were summarized by Kamimura (1966). Rather than interpret the decline in apparent abundance as linear Suda indicated that the decline was quite rapid during the early 1950's, but by the mid-1950's the decline halted and CPUE became stabilized at a relatively low level. A rapid decline followed by a stabilization of CPUE implies that the regression of CPUE on time should be curvilinear. We have already indicated that there is some evidence for curvilinearity. In addition it is quite obvious that a linear decline in apparent abundance could not last for an indefinite period of time without the stock of fish becoming extinct. In one sense the question of linearity or curvilinearity is somewhat academic for our data since both methods should yield declines in apparent abundance that are of the same order of magnitude. This implies, of course, that estimates of the coefficient of total mortality based on either the linear or curvilinear interpretation of the decline in CPUE should be roughly equal. But

our crude estimate of the total mortality coefficient in 1961 was 1.3 whereas that reported by Kamimura (1966) is 0.4. We cannot explain this discrepancy except to note that the computations reported by Kamimura were undoubtedly based on a longer series of data than was used by us. We must also emphasize that an increase in the per-head rate of death of 0.1 fish per year with a constant instantaneous coefficient of natural mortality and a constant catchability coefficient implies that effort is increasing as a function of the reciprocal of the catchability coefficient. Without knowing the trend in effort, however, it is difficult to tell the extent to which a trend in CPUE is related to changes in effort or changes in the catchability coefficient.

With constant growth coefficients, constant recruitment, age, etc., an increase in the per-head rate of death implies that the average age and therefore, also, the average size of albacore taken by the longline fishery should decrease. Such a reduction in average age is shown by Suda (1959). This reduction can also be seen, qualitatively, in a later study by Suda 1963b: p. 1250). On the other hand, we have averaged the length-frequency samples given by Suda (1963a) and find no conspicuous decrease in average size. If growth rate is constant, and we have no information to the contrary, then according to the longline-fish average lengths depicted in figure 5, average age is not decreasing. We have also examined these data by 10° longitudinal strips and also find no decreasing trend in average size within a longitudinal strip, which reduces the possibility that the absence of a declining trend in size could be related to the manner in which the size distributions are weighted. Another consideration is that the longline gear may be highly size selective. If this were true, then a decline in average size in the population would not change the average size of the fish in the catch, but it would reduce the catchability coefficient so that the decline in CPUE would be greater than the decline in abundance of the population. A final consideration concerns the underlying possibility of the curvilinear decline in actual abundance that was discussed earlier. An exceedingly rapid--fishery induced--initial decline in apparent abundance might produce a sharp initial decline in average size which may appear to be a random fluctuation. Thus, a real trend may be masked--especially for such a short series of data--by a fortuitous combination of time-dependent parametric changes and random fluctuations. Thus, while the decline in apparent abundance certainly suggests a decline in actual abundance. an assessment of the magnitude of this decline awaits further studies on size-distribution and fishery intensity.

Spatial Statistics

The next question that we considered in our study was the relation of the declining apparent abundance of albacore to the temporal-spatial distribution of the albacore on the longline grounds. In order to investigate the temporal-spatial distribution of the albacore we computed the spatial statistics. The spatial statistics revealed several interesting characteristics of the apparent distribution of albacore in the North Pacific.

First, as indicated previously, the spatial statistics for catch and CPUE were nearly identical. This agreement implies that the spatial distribution of catch is coincident with the spatial distribution of apparent abundance. The statistics for effort, however, are not coincident with those for catch and CPUE. The fact that catch and CPUE are very nearly coincident and that effort is not centered on either indicates that the fishery is operating efficiently in the sense that the catch is taken from the area where apparent abundance is most highly concentrated and that the fishing effort considered in this study is not totally directed toward catching albacore. The fact that the spatial distribution of the albacore's apparent abundance is nearly constant for any month and that of effort is not constant, but moves away from the center of albacore apparent abundance, reflects the increasing tendency for Japanese longline effort to move away from the northwest Pacific Ocean. The tendency of longline effort to move from the northwest Pacific toward the southeast Pacific during the study period is well known (e.g., Rothschild, 1966). The tendency for effort to move away from the major apparent concentration of albacore in the northwest Pacific would naturally introduce a declining trend in albacore apparent abundance that merely reflects the change in the distribution of effort in the North Pacific Ocean rather than any actual change in albacore abundance. This situation cannot be studied in detail owing to lack of data on the other species. We believe, however, that the problem of effort moving from the albacore grounds as well as the

problem of competing species (Rothschild, 1967) as they affect albacore apparent abundance on the longline grounds are, to a degree, obviated by considering, as we have done, trends in apparent abundance in the albacore area only (fig. 4).

Thus, the spatial statistics give not only measurements of the spatial attributes of the albacore distribution, but, from the interrelations among the spatial statistics for catch, CPUE, and effort, they also give clues on changes in efficiency (the maximum efficiency occurs when catch, CPUE, and effort are coincident) and catchability. Emphasis must again be placed, when considering the relative position of the spatial statistics for catch, CPUE, and effort, on the "apparent" rather than "absolute" nature of the spatial statistics. For example, if effort covered only a small portion of the albacore distribution (an unlikely situation) then the spatial first moment, for example, would be a biased estimate of the first moment of the albacore distribution, and in such a situation the estimated dispersion would be less than the actual dispersion. Perhaps a more likely source of bias than that produced by an incomplete spatial coverage of the fishable population by effort may arise from a variable catchability of albacore over the fishing ground. Therefore, any observed spatial distribution may contain components owing to (1) the actual distribution of the fish, (2) the gear not actually covering the fishing area, or (3) situations that cause catchability to vary over the fishing grounds.

Secondly, a very striking feature of the albacore data is the year-to-year constancy in catch and CPUE spatial statistics. The constancy implies that the spatial statistics for any year can be predicted with a high degree of accuracy. This point is demonstrated for the two-dimensional first moment in figure 15. We expected that the spatial statistics would be much more variable than they actually were. Our expectation was based on an assumption that variations in the spatial statistics would be influenced to a large extent by variations in the oceanic environment. Examples of environmental variability, especially in surface waters, are quite common in such things as "warm years," "cold years," and vagaries in the position of the Kuroshio axis, for example. We conclude from the relative constancy of the spatial statistics, that either the environment is not as variable as we may have thought (possibly owing to the albacore being caught at depths by the longline gear where the environment is, in actuality, relatively more constant than that at the surface), or that any changes in the environment that do occur have little effect upon the distribution of the albacore, or that the effect of the environment on the fish is masked by random or unexplained variability. Thus, any deviation in spatial distribution from the long-term average appears to be so small that it would be difficult to associate it with a biological cause. From a practical point of view, in terms of searching for albacore, the deviations are so small that they are rather unimportant.

Third, it might be expected that a decline in apparent abundance of the magnitude observed for the albacore would be associated with large changes in spatial statistics. For example, since there is some size stratification on the longline grounds (Suda, 1963a), an alteration in the average size of fish caught would produce a modification in the two-dimensional first moment. As we have pointed out, however, the evidence on trends in average size of albacore for the study period is equivocal. Also a decline in apparent abundance might be expected to produce a contraction in the horizontal space occupied by the albacore. The virtual constancy of the spatial statistics, however, suggests that there is no large change in the spatial statistics during the study period, and therefore the decline in apparent abundance was not related to large changes in the spatial statistics.

The Environment and Anomalies in Catch-per-unit-of-effort and Spatial Statistics

Despite the clear trend in declining CPUE and the constancy of many aspects of the spatial statistics certain years were anomalous with respect to trends and variations in these indices. In CPUE for example, 1948, 1952, 1953, 1954, 1958, and 1961 were above the regressed average, but 1949, 1950, 1951, 1955, 1956, 1957, 1959, and 1960 were poorer than the regressed average.

With respect to anomalies in spatial statistics, the first moments for CPUE in 1954 and in 1955 were to the north of the long-term first moment and in 1957, 1959, and 1961 to the south of the long-term moment (fig. 15). Another example of deviations, which are rather small for practical purposes, may be found in the significant long-term trends in the spatial statistics: CPUE moved in a southerly direction,

catch moved toward Japan, effort expanded longitudinally, and effort continued to increase in negative rotation during the study period. Another example of a trend might be found in the tendency for the velocity of the apparent movement to increase during the study period.

These anomalies may result to some extent from variability in the oceanic environment. The problem of relating the abundance and distribution of fish to changes in the oceanic environment (we use the term oceanic environment in the abstract sense to denote the set of all variables with which the albacore coact or react as well as the variability of each and its correlation with other members of the set) is fraught with difficulties involving the measurement of the true abundance and position of the fish. In addition, it is difficult to determine which subset of the many environmental variables is actually most relevant in determining the distribution or abundance of the fish, to develop methods of measuring the appropriate subset of these variables, and finally to develop techniques for the study of the relation between the abundance and distribution of fish and the relevant variables of the environment.

Some progress has been made in this study toward measuring the apparent abundance and apparent spatial distribution of the albacore, but we have not furthered an understanding of the complex interrelations of the albacore and its environment beyond some of the study on the correlation between apparent abundance of albacore and sea-surface temperature (Johnson, 1962). Instead, however, we will mention briefly some of the concepts that have given us difficulty in supporting our empirical observations by a cause and effect relationship. For simplicity we will relate our discussion to temperature but it could relate equally well to any other variable or combination of variables, again not only with respect to the absolute levels of the variables, but also to their variability and their mutual intercorrelations. The problem of measuring temperature in a way which is appropriate for fishery investigations has been discussed by Bell and Pruter (1958). For the albacore problem we would need to estimate the average temperature for each 10° quadrangle of the North Pacific Ocean for some finite time period. But there are at least two, probably omnipresent, sources of bias in estimates of the average temperature of a 10° quadrangle of ocean. The first source of bias arises from the logistic constraints of practical vessel tracks that prevent taking a random sample of temperatures in the quadrangles of interest. Even an average temperature based upon a more practical systematic, rather than random, sampling plan--even ignoring the mathematical bias that is sometimes inherent in systematic sampling designs (see Cochran, 1953)--can be severely biased. The extent of the bias would depend on the thermal gradient and whether the cruise track was parallel or normal to the isothermal lines. It is in fact rather intriguing to consider that some features depicted in oceanographic atlases may be charted in a position that is dislocated owing to the direction of the cruise track. The second source of bias involves determining the locations of those temperatures that are within the cube of water that are actually relevant to the behavior of the fish. In some instances surface temperatures may be relevant; in others, temperature at some constant depth, or possibly even temperatures on a surface of constant dissolved oxygen or density.

Another difficulty in interpreting the relation between the distribution and abundance of fish and the oceanic environment is that a fish's response to the environment is time-dependent and not time-independent as is usually implicitly assumed when relating ocean temperatures to fish distribution. The time-dependence is a compensatory phenomenon in which an animal's lethal temperature or temperature preferendum, for example, is a function of its past thermal history. Pioneering studies of this "physiological memory" were accomplished by Fry (1947). Over the subsequent two decades there have been many studies of the compensatory process. Most of these studies have been of acclimation, which refers to compensatory changes that organisms undergo in response to changing levels of an environmental variable under simplified laboratory conditions, but not of acclimatization which refers to the compensatory process under the more complex, and of course more realistic, natural situation (see, e.g., Hoar, 1966: p. 296). Although acclimatization has not been studied for the albacore it almost certainly operates and influences thermal and other preferenda of the albacore. While acclimatization may produce small changes in temperature preferendum, these small changes could involve rather large horizontal distances. Although the nature of the acclimatory period with respect to intensity and duration of exposure of an organism to various levels is not

completely understood, it seems entirely probable that to understand an organism's response to temperature at a contemporary instant we must consider in addition to absolute temperatures the derivatives with respect to time and space of temperature. Even in a simplified univariate situation a knowledge of the thermal history of a fish would be difficult to obtain.

Despite the difficulty in obtaining information on acclimatization it appears that this phenomenon may very well operate in tunas and may provide at least a partial explanation for the albacore being taken in waters of the Japanese fishery that are several degrees cooler than those in which they are taken in the North American fishery. Even within the eastern Pacific fishery the apparent temperature preferendum appears to be related to the size of the albacore. The differences in apparent temperature at different locations and at different sizes or ages are probably related, to some extent, to acclimatization phenomena. Thus, with even a variable that is as relatively simple to measure as temperature, many conceptual problems still need to be resolved in order to understand the causal nature of spatial distributions with respect to temperatures and other environmental or sets of environmental variables.

Migratory Route

An understanding of the migratory route of the albacore among the three fisheries of the North Pacific Ocean is of crucial importance to understanding the dynamics of the albacore. Knowledge of the migratory route is needed to estimate age-specific fishing mortality and also to understand the manner in which events in each fishery affect events in other fisheries. For example, if, as we postulate in this paper, an important segment of the albacore escapement from the North American fishery becomes vulnerable to the pole-and-line fishery before it becomes vulnerable to the longline fishery, then an understanding of the changes in abundance, and the amount of fishing effort exerted in the pole-and-line fishery is crucial to obtaining an understanding of the causes of the decline in apparent abundance in the longline fishery. Another example of how the dynamics of the albacore in one fishery might affect the dynamics of the albacore in another fishery is provided by data given in Clemens and Craig (1965). If we take their data at face value, we find that in their figure 96, the California fishery after 1950 exhibits (1) a decreasing trend in catch, (2) a decreasing trend in effort measured in number of boat-months and in number of boats, and (3) an increasing trend in catch per boat-month. For steady-state recruitment into the California fishery and no trends in catchability coefficient, etc., their data imply an increasing trend in escapement from the California fishery. If, in fact, there is an increasing trend in escapement and all other things are equal, the recruitment to the Japanese fisheries must be increasing. We conclude (on the basis of accepting the simplifying assumptions that catchability for the California fishery is constant, etc.) that a consideration of a declining apparent abundance of the longline fishery must include the evidence that this decline occurs in the face of an increasing trend in recruitment to the Japanese fisheries. This consideration must also include an understanding of the predominant route of the albacore because the effort of an increasing trend in recruitment to the Japanese fisheries upon the longline fishery would depend, to a large extent, on whether the recruited fish first enter the longline or the pole-and-line fishery.

Although we have emphasized the North American to pole-and-line to longline migratory route we should stress that the reasoning that we have used to support this pathway has a possible internal inconsistency. This inconsistency arises between the migratory-route evidence based upon the relation of time between middates of each fishery and growth estimates (fig. 18) and the ratio of longline to pole-and-line tag recoveries (fig. 16). The good agreement between the expected sizes based on middates between fisheries and growth rate and the actual average size depicted in figure 5 suggests that the entry of any albacore into the longline fishery before the pole-and-line fishery is unlikely. On the other hand, the rather limited tagging data indicate that somewhat less than half of the albacore enter the longline fishery before the pole-and-line fishery, implying that the longline fish should have an average length of about 81 cm. Since our information on average size, growth rates, middates of fishery, and proportion of tag recoveries is collectively not very precise, an interpretation of this possible inconsistency must await further study.

Evolution of Migratory Pattern

The apparently well-defined migratory route of the albacore invites speculation on the mech-

anisms that generate the space-time distribution of fish. Of particular interest is the situation where the spatial distribution is not fixed during the fish's lifespan and the fish undergo movements or migrations that are specializations of a more sedentary behavior. We would postulate that these specializations have resulted from a necessity for fish to ingest, on the average, an amount of food that supplies to the fish at least as much energy as that required for maintenance and growth. But the food resources within the distributional ranges of some fishes tended--during the course of evolutionary time--to become inadequate for certain life-history stages. This inadequacy probably arose from either modifications in the environment or from morphological or physiological specializations. Some forms were able to "escape" from the areas of inadequate forage resources by evolving a migratory behavior. The purpose of this section is to discuss the mechanisms by which this migratory behavior could have become established.

For this discussion the position of fisn or their forage will be defined on a field of space-time points. Each space-time point is indexed by discrete elements of latitude, longitude, depth, and time. Further, the discussion is based on the axiom that a fish needs to ingest a sufficient amount of food to supply it with sufficient energy to survive in its ecosystem (survival in the ecosystem being distinct and having different requirements than survival under laboratory or other artificial conditions). If a fish has survived to some particular time point in the ecosystem, then it obviously must have survived at all time points previous to the particular time point and subsequent to its birth. In order for a fish to exist at a particular space-time point, it must be able to ingest at least as much energy as is required for its survival at that space-time point or be able to draw on energy stores that were acquired at some previous space-time point. If a fish obtains energy by ingesting a more or less steady supply of forage at a particular space point, then it can remain at that space point for an indefinite period of time. If however, a fish cannot obtain forage at a particular space-time point it must eventually find a space-time point at which it can obtain forage or it will succumb either from starvation, or, more likely, from its inability to cope with the requirements of its ecosystem.

Whether or not a fish obtains the forage required for its survival in the ecosystem at any particular space-time point depends on the quality or the structure of forage at any particular space-time point. The quality of the forage, in terms of its ability to provide energetic sustenance for the forager, is represented by the concept of a forage lattice. A forage lattice is simply a three-dimensional array of lattice points. Each lattice point is occupied by a packet of energy in the guise of a forage item or forage items which could be ingested and utilized as energy by the forager. The spacing between the lattice points is not measured in conventional metric terms of distance, but rather in terms of the difference between the energy available at each lattice point and the energy required for the forager to swim between and ingest food at the lattice points. Thus, it is conceivable that lattices of high forage density might be able to support, energetically, less foragers than lattices of lower density owing to a possible higher energy content at the lattice points of the lower density lattices.

The existence of several types of forage lattice becomes clear. First, there are suitable and unsuitable lattices. The suitability of a lattice at a space-time point must be expressed in terms of the metabolism and behavior of the species of interest considering all effects on the metabolism that are specific with respect to the contemporaneous, as well as to past, effects of size, age, sex, etc. For example, a forage lattice of diatoms might be suitable for copepods, but not for tunas. Or a forage lattice that has its lattice points occupied by small fishes and squids might be suitable for larger tunas whereas a forage lattice of copepods might be necessary to support juvenile tunas. Thus, a particular space-time point may contain several lattices. Of these several lattices, one may be suitable for the forager of interest. The unsuitable lattices are irrelevant to our problem in the sense that they have relatively no greater effect on the forager. In another sense the unsuitable lattices are highly relevant since they define the trophic structure of the community. Second, of the suitable lattices, there is one that is at least optimal; the other suitable lattices are suboptimal. An optimal lattice is one in which the distances between the lattice points is such that the energy expended to swim between the lattice points is less than the energy which can be ingested at the lattice points. By contrast, obtaining more

energy from ingestion in a suboptimal lattice than that required to swim between the nodes is not possible. While it is obvious that a fish can remain in a suboptimal or unsuitable lattice for a relatively short period of time, a fish can remain in an optimal lattice indefinitely.

Let us now set our fish forage lattice system in motion. First, we consider only space-time points that are contained in a region where the physical environment is tolerable for the species of interest. Next, we find a set of space-time points that contains suitable and most likely optimal lattices for both spawning parents and progeny. Now we reiterate that the space-time points are simply fixtures in space but the quality of a forage lattice depends upon the physiology, behavior, and density of the forages of interest. Migration becomes necessary when fish are forced to venture from space points that are optimal. "Leaving" optimal space points probably occurs in two general ways. In the first, the forage structure at a space point remains essentially constant over time, but as a fish grows the forage lattice at the space point becomes nonoptimal owing to size- or age-specific food habits on the part of the forager. In the second, a space-time point that has an optimal lattice has its lattice modified owing to seasonal changes, intraspecific competition, or even the predatory effects of the forager upon the forage.

Thus, the causal mechanism for movements and migrations would appear to involve, rather intimately, the temporal-spatial distribution of suitable energy as well as the energetic demands of the forager--both in terms of the quantity of energy and the quality of energy (i.e., the animal must be able to catch and ingest the "energy"). As some relatively sedentary fish evolved and developed specializations, their forage requirements and available forage became modified. In order to obtain sufficient energy resources the fish needed to evolve a behavior where they could continually optimize the forage lattice. The result of the sequential optimization procedure is migration, which as we have shown in this paper, is highly developed in the albacore of the North Pacific Ocean.

Possible Genetic Effects of Fishing

Another question of interest in considering large fishery-related declines in the abundance of fish stocks--such as those that might be implied by the decline in apparent abundance of the albacore--concerns the effects of fishing on the genetic structure of the fish populations. Modification of the genetic structure of a population could result from fishing through some form of genetic selection.

Before we consider genetic selection per se, let us consider selection in general. We define selection in the context of a sampling procedure. If sampling is random, then selection does not operate. If the sampling procedure is not random then selection operates. In nonrandom sampling those elements in the population that have a relatively high probability of being included in the sample are positively selected and those that have a low probability of being included in the sample are negatively selected.

Selection must operate with respect to some attribute or set of attributes of the individuals that are to be sampled. As an example, the examination of a sample of fish by a biologist might be considered as a multistage sampling process in which the selection attribute is the length of the fish. Thus, nature might take a nonrandom sample from the population and place it on the fishing grounds; then the fishing gear might select a nonrandom sample of the fish on the fishing grounds; and then the biologist samples the fish that are caught (it is interesting to note that in many fisheries it is practically impossible for a biologist to take a truly random sample of fish).

If the attribute or set of attributes involved in the fishing-selection process is genetically controlled, then it is implicit that fishing will remove certain phenotypes from the population at the expense of those genotypes that are either unselected or negatively selected. Suppose, as we have postulated, that a fish's existence at a particular space-time point is the result of some genotypic expression. Thus, in the albacore, we would postulate that its migration pattern is the result of some genetic expression. Basically, the albacore fishing operates at three stations along the migratory path of the albacore. The majority of the albacore appear to migrate through these stations. If the majority of albacore actually do migrate through these stations and the act of migration through the stations is ascribable to a different genetic structure than that which is maintained in individuals that do not migrate through one or more of these stations, then it is clear that a positive genetic selection is being exerted on the individuals that migrate through the stations. Further, it is the genetic constituency of the albacore population which, given a sufficient

fishing intensity and number of generations, would be modified. The consequences of this modification would be a reduction in CPUE on the fishing grounds, but not a reduction in abundance or population size. There are many other conceivable attributes besides migration which could be genetically controlled and selected by fishing.

The discussion of the effect of fishing on the genetic structure of the population raises the question of whether fishing selection might to some extent replace natural selection. The answer to this question would be affirmative in the sense that, according to the theory of fishing, fishing mortalities increase the mortality rate and in some situations fishing deaths might even exceed the natural deaths in the unfished population. In fact, fishing might even be more selective (in the sense that the act of fishing imposes a greater probability of capture of individuals with certain genetically controlled attributes) than natural deaths. We can envision that all fishing deaths could result from a monolithic type of selection. In an unfished population, however, the deaths would tend to be from a variety of causes that might even cancel one another. A monolithic type of fishing selection then might to a large extent replace or modify natural selection. The added selection from fishing might have dire consequences upon the population. These dire consequences would result from an elevation in selection such that its cost (see Haldane, 1957) would be in excess of that which could be tolerated by the population in the face of other environmental demands for genetic plasticity. Thus, such a phenomenon could account for some of the catastrophic declines in fish population size in which (even under very high fishing pressure) the decrements in the population owing to fishing deaths are considerably less than the total deaths in the population. It must be emphasized that the key to the whole selection argument involves the nonrandom removal of certain genes from the population. If we examine the life history of any fish, then we see that the greatest opportunity for the selective removal of genes from the population is during the first few months of life when upwards of 99.5 percent of any cohort usually dies. Thus any fishing or natural genetic selection that operates during the adult stages of life might be relatively unimportant when compared with the natural selection that might operate during a fish's larval existence. Further, many fishing operations, in contrast to that for the albacore in the North Pacific, operate on the population after some spawning has taken place. In these instances, the effects of fishing genetic selection would be materially reduced.

SUMMARY REMARKS

A decline in the apparent abundance of albacore in the North Pacific longline grounds is evident. Effort statistics do not appear sufficiently precise to quantitatively relate to this decline. The decline does not appear to be related to changes in average length for the data which we have available nor do the positive and negative deviations from the long-term trends in any year appear to be related to fluctuations in size for that year. Thus, the evidence that these deviations might owe to fluctuations in year-class strength is not strong. Based on the migratory route postulated in this paper, the fishing intensity in the pole-and-line fishery might have a stronger effect on the longline fishery than fishing effort in the longline fishery per se. If the longline fishery is strongly size-selective then an increased fishery-induced mortality rate would reduce the average size of the fish in the population and the consequences of this reduction would be a reduction in longline CPUE without a reduction in average size. The complicated interactions of the various fisheries make the assumptions used for computing the usual steady-state rates tacit oversimplifications. The spatial statistics also do not show any obvious relation to the changes in CPUE. The spatial statistics do indicate, however, interesting features of albacore biology. These features involve the predictable spatial position of the albacore, which suggests need for a detailed study of the biological and physical oceanography of the area that the albacore move through, and the relatively slow rate of apparent motion, which suggests, upon comparison with the relatively rapid velocities that tuna are capable of achieving, that the path of the albacore on the longline grounds is essentially nonlinear. This nonlinear path may indeed, be highly convoluted, a circumstance which could account for a higher rate of hookfish contacts.

The key to understanding the dynamics of the reaction of the various North Pacific fisheries for albacore upon fishing depends to a large extent in understanding the amounts of fishing intensity applied to each age group. In order to

do this we need a better understanding of the migratory route of the albacore in the North Pacific Ocean. We have provided evidence for a simplified version of a fishery-specific route where the predominant movement of the albacore is from the North American fishery to the pole-and-line fishery to the longline fishery.

The migratory route of the albacore and the changes in apparent abundance encourage speculations on the mechanisms of migration and the possible effect of fishing on the genetic constituency of exploited populations which we provide.

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